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An Assessment of the Trapping Web for the Density Estimation of Small Mammals

Thomas J. Maier
University of Massachusetts Amherst

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AN ASSESSMENT OF THE TRAPPING WEB
FOR THE DENSITY ESTIMATION OF SMALL MAMMALS

A Thesis Presented

by

THOMAS J. MAIER

Submitted to the Graduate School of the
University of Massachusetts Amherst in partial fulfillment
of the requirements for the degree of

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Wildlife and Fisheries Conservation

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THOMAS J. MAIER

Approved as to style and content by:

Jay B. Hestbeck, Chair

Richard M. DeGraaf, Member

John T. Finn, Member

William C. McComb, Department Head
Department of Natural Resources & Conservation

“But, Mousie, thou art [not alone],
In proving foresight may be vain:
The best laid schemes o’ mice an’ men
 [Go oft askew],
An’ lea’e us nought but grief an’ pain
 For promis’d joy.”

Robert Burns, ca. 1785, excerpt from “To a Mouse,
on Turning Her Up in Her Nest with the Plough...”

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Special thanks are reserved for Kate Doyle for her assistance in practically every aspect of this project—her patience and advice were appreciated—and my family and friends, all living “out West”, for their forbearance in my being “back East” so long. Finally, I thank S. Cooter, along with his numerous cohorts, for ethological instruction.

ABSTRACT

AN ASSESSMENT OF THE TRAPPING WEB FOR THE DENSITY ESTIMATION OF SMALL MAMMALS

MAY 2003

THOMAS J. MAIER, B.S., ST. CLOUD STATE UNIVERSITY
M.S., UNIVERSITY OF MASSACHUSETTS AMHERST

Directed by: Professor Jay B. Hestbeck

Investigations in various fields of research require reliable population density estimates of small mammals. Such estimates allow the direct comparison of independent experimental results and statistical synthesis via meta-analyses, thereby broadening our ecological knowledge. The reliability of traditional density estimation techniques is uncertain, because procedures by which the effective area of open, unbound populations may be determined have not been satisfactorily developed. To circumvent this problem, Anderson and others (1983) proposed a distance-sampling method (the “trapping web”) that provides a direct estimate of population density without requiring an area estimate; yet, its use has been infrequent.

A literature review suggests that non-use or unsuccessful use of the trapping web is due to the large effort required (big grids, many traps) and/or low individual captures; as such, further work is needed to establish how small a trapping web will perform well. Nonetheless, other more fundamental work seems more important initially. Using data

representing a wide range of murid population densities from seven forested sites in central Massachusetts, 1996-98, I assessed the movement of individual white-footed mice (*Peromyscus leucopus*) captured on trapping webs to determine the effect of the method's inherent trap/bait gradient. I also evaluated variation in capture probability (heterogeneity) for these mice and southern red-backed voles (*Clethrionomys gapperi*) to elucidate this behavior's effect on trapping web estimates. Finally, I compared trapping-web estimates to density estimates derived from mark-recapture grids for the same populations to assess method performance.

Mice were apparently displaced toward trapping web centers; such movement likely exacerbates edge-effect, limits the duration of trial periods, complicates use of web recapture data, and potentially biases density estimates. Heterogeneity had no effect on estimates for either murid, making the post-stratification of data unnecessary. Comparison of density estimates suggests systematic differences in method performance relative to population levels; CAPTURE estimates appeared positively-biased at low- to mid-level densities, whereas DISTANCE estimates appeared positively-biased at the highest population densities observed. Although not without problems, the trapping web method, with its amplitude of trap distances, may prove useful in determining optimal trap spacing; thus providing a long-sought, empirically-defined trap-spacing index specific to small mammal species and habitats.

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CHAPTER 1

THE TRAPPING WEB: A REVIEW, OBJECTIVES, AND GENERAL METHODS

Introduction

Recent investigations in various fields of research, including landscape ecology, population genetics, ethology, and evolution, have emphasized a need for reliable density estimates of small mammals (Stenseth and Lidicker 1992). Density estimates, i.e., the estimated population within an estimated effective area ($\hat{D} = \hat{N} / \hat{A}$), permit both direct comparisons of results of independent experiments and statistical synthesis by meta-analyses, thereby increasing our knowledge of broader ecological patterns (Gurevitch and Hedges 1993). Moreover, the very concept of density is integral to any analysis, description, or discussion of population dynamics.

The reliability of traditional, small-mammal density-estimation techniques may be questioned. Population (N) estimation techniques have proliferated during the last 60 years (see Seber 1992, Lancia et al. 1994). Nevertheless, comparisons of \hat{N} between individual studies are largely meaningless without some reference to the effective area of a population (Anderson et al. 1983, Wilson and Anderson 1985a), and procedures by which the effective area (A) of an open, unbounded population may be determined have not been satisfactorily developed. For example, the most common method currently used to assess effective area is based on Dice's (1938) concept of a boundary strip (W) added to a trapping grid, where the width of W equals half of the mean maximum distance moved (hereafter referred to as "MMDM") by members of the

population of interest. Dice (1941) emphasized the subjective limitations of this method and, more recently, this method of using MMDMs has been shown to inadequately represent the movement of small mammals (e.g., Parmenter et al. 2003).

In an attempt to circumvent the problems inherent to assessing effective area, Anderson et al. (1983) proposed a trapping method (hereafter referred to as the “trapping web” or “web”) based on distance-sampling theory that provides a direct estimate of small mammal density without requiring an estimate of effective area (see Appendix 1-A for assumptions). Use of the trapping web, however, appears to have been infrequent since its introduction in 1983, even though its advantages include: easy setup and use (e.g., animals do not need to be individually marked), reasonable density estimates derived from as few as 60 individual captures, and relaxed assumptions regarding closure and the capture probability of individuals (Anderson et al. 1983). Further, the trapping web has proved robust when evaluated using Monte Carlo methods (Wilson and Anderson 1985a), has been favorably compared to mark-recapture nested grids using the same population of meadow voles (*Microtus pennsylvanicus*; Jett and Nichols 1987), and potentially validated against known populations of darkling beetles (Tenebrionidae: *Eleodes* spp.; Parmenter et al. 1989). Additionally, the technique has been re-described and its use clarified in numerous texts (e.g., Buckland et al. 1993, Lancia et al. 1994, Nichols and Dickman 1996). Despite these advantages, supportive comparisons, and multiple descriptions of the trapping web’s potential use, the method has apparently been used infrequently.

Literature Review

Trapping webs were used for the direct estimation of population density in only 10 of 30 papers that addressed the method (Parmenter et al. 1985, Parmenter and MacMahon 1988a, Parmenter and MacMahon 1988b, Ebert and Kondratieff 1992, Creekmore et al. 1994, McIntyre 1995, Seidel and Whitmore 1995, Ellis et al. 1997a, Corn and Conroy 1998, Parmenter et al. 2003). Of these 10 papers, three used trapping webs to estimate densities for insects that do not maintain home ranges or territories (Parmenter and MacMahon 1988a, Ebert and Kondratieff 1992, McIntyre 1995), a use for which the method was neither designed (Anderson et al. 1983) nor considered appropriate (Buckland et al. 1993:283).

As to the other 20 papers that either used the trapping web without producing density estimates or cited the method without using it, the following reasons were given: 1) trapping webs required too large a grid or habitat size constraints prevented their use (MacMahon et al. 1989, Hartman and Krenz 1993, Ellis et al. 1997b); 2) arboreal small mammals in the tropics that naturally occur at low densities require less intensive, less time-consuming methods (i.e., than the trapping web) to maximize the number of species captured (Mares and Ernest 1995); 3) a single web per treatment area and collection period did not allow “statistical comparison” (Fair et al. 1995a); 4) there were insufficient data collected (i.e., too few individual captures on trapping webs) for density estimation (MacMahon et al. 1989, Fair et al. 1995a, Fair et al. 1995b, Graham and Chomel 1997, Stapp 1997, Ellis et al. 1997b, Swann et al. 1997, Cutler and Morrison 1998, Parmenter et al. 1998, Smith et al. 1998, Abbot et al. 1999, Parmenter et al. 1999); and finally, 5) trapping webs were either used as sample units for other

measures because of conjoining small mammal research (Kieft et al. 1998), or briefly mentioned or discussed within a review (Smith and Urness 1984, Seber 1986, Seber 1992, Skalski 1994, Crist and Wiens 1995).

The primary reasons for the non-use or unsuccessful use of trapping webs would thus appear to be associated with the perceived effort required (i.e., large grids [2-3 ha] and number of traps [T]) and/or low catches of individual animals. Anderson et al. (1983:fig. 1) offered a trap layout design for a single trapping web that consisted of 16 lines (hereafter referred to as “radii”) with 20 traps each, totaling 320 traps. Although this large number of traps for a single trapping web is not mandatory, Anderson et al. (1983) tentatively recommended $T > 250$ and Buckland et al. (1993) recommended $T > 200$. That the recommended trapping web configuration is perceived to require too great an effort is supported by the fact that, of the 12 papers cited above as having insufficient data to estimate densities, all used trapping webs that were of less effort (i.e., fewer traps) than the design suggested by Anderson et al. (1983). Further, 60 individual captures may be difficult to attain if trapping webs are too small (and/or population densities are very low). Many small mammal species generally exist at relatively low population densities in certain habitats, such as tropical gallery forest (e.g., Mares and Ernest 1995) and desert (e.g., Parmenter et al 2003); as such, such habitats may require larger trapping webs. Additional reasons for the non-use of trapping webs may include: 1) subjective forms of analysis involving the truncation of data (Link and Barker 1994); 2) optimum web size, trap numbers, and trap inter-spacing may vary by species (Parmenter et al. 1989); coupled with 3) a lack of

successfully analyzed empirical data for a gradient of small mammal population levels (Buckland et al. 1993:313; Mares and Ernest 1995).

What further assessments might be made of the trapping web to refine its potential? Certainly, as indicated by the many failed attempts using insufficient webs, further work is needed to establish how small a trapping web will perform well at various density levels (Wilson and Anderson 1985a). Other more fundamental work, however, such as establishing that animals are not displaced or attracted toward trapping web centers given the concentrations of traps and bait or, conversely, driven off by human activity, would seem more important initially. Also, assessment of how the gradient of trap densities inherent to trapping web design and how its potential variation in the capture probability of animals may affect analyses seems required. Finally, comparisons of the trapping web with other population density estimation methods, such as mark-recapture, with empirical replication over a wide range of small mammal density levels are needed (e.g., Jett and Nichols 1987, Parmenter et al. 2003). These areas of work on the use of the trapping web are by no means exhaustive; as stated by Thomas et al. (2002), “There is still much to be done...the subject [design based on distance sampling theory] is still a lively one for statistics and ecology.”

Objectives

1. Assess the movement of individual small mammals captured on trapping webs (see Chapter 2). Concentrations of baited traps toward web centers may attract or conceivably repel animals (e.g., the latter due to prolonged human presence/activity and/or the destruction of vegetation/micro-habitat). More simply however, given the vagility of small mammals, the greater probability of their capture near trapping web

centers, and numerous observations that many small mammals often do not enter the live-trap(s) they encounter for some time, both the initial capture and subsequent recapture of animals may result in their mechanistic “displacement” towards trapping web centers; such movement would violate the second assumption required of the trapping web distance-sampling design (see Appendix 1-A).

2. Assess the effects of heterogeneity on density estimates (see Chapter 3). The trapping web design neither entails specific assumptions regarding heterogeneity nor requires knowledge of capture probability models; most sources of heterogeneity are considered to contribute little to bias provided all animals of interest are detected at web center. Nevertheless, it is unclear why heterogeneity on trapping webs is considered unimportant, given that heterogeneity in other types of distance sampling data is commonly dealt with by stratification or use of covariates.
3. Compare web-generated density estimates to those derived from mark-recapture over a range of population density levels (see Chapter 4). Estimates from empirical trapping web data have not previously been evaluated over the entire range of population densities possible for small mammals; these results will permit inferences about the potential performances of both methods for a wide range of field situations.

General Methods

Trapping sites, located in central Massachusetts on state lands managed by the Metropolitan District Commission to provide water for the Boston municipal area, were all mature forests (> 80 years old) of the red oak (*Quercus rubra*)-white pine (*Pinus strobus*)-red maple (*Acer rubrum*) forest-cover type (Eyre 1980). These sites were live-

trapped between August and December 1996-98, given that small mammal populations are often largest during this period, on an annual basis. (Terman 1968:418).

Trapping efforts focused on white-footed mice (*Peromyscus leucopus*), based upon this species' ubiquity and often high abundance within oak (*Quercus* sp.) woodlands (Baker 1968:100), the ease with which the species is live-trapped (see Tanaka 1963:fig. 1), and its importance in both ecosystem (Elkinton et al. 1996) and human health (Jones et al. 1998). Data from southern red-backed voles (*Clethrionomys gapperi*) were also examined when they were trapped in sufficient number, because their response to traps may differ from that of mice (Parmenter et al. 1989).

Small mammals were captured in 8 x 8 x 24-cm Sherman live-traps (H. B. Sherman Traps, Tallahassee, FL) containing dry, non-sterile cotton for bedding, and baited with a mixture of peanut butter, oatmeal, and bacon fat. Traps were covered with leaves and forest litter to protect occupants from the elements, and checked daily. Captured small mammals were individually tagged with small, uniquely numbered ear tags (#1005 size 1 Monel, National Band and Tag Co., Newport, KY). Data collected included site name, date, observer, census day, trap station, species, tag number, capture class (i.e., whether new capture or not), age, sex, reproductive condition, ear tagged (right-left), weight, and pertinent comments. Processed animals were released at their point of capture.

I followed guidelines for the capture and handling of mammals as approved by the American Society of Mammalogists (ASM 1998). Scientific collecting permits were secured from the Massachusetts Division of Fisheries and Wildlife. The University of Massachusetts at Amherst Institutional Animal Care and Use Committee

(IACUC) approved protocol #18-02-01 for this study. All small mammal mortalities were deposited in the Vertebrate Museum of the University of Massachusetts, Amherst.

Given the difficulties experienced by previous studies attempting to use either too small a trapping web and/or too few traps, webs used in this study were all ca. 3-ha and generally comprised of 16 equidistant radii (the latter parameter, as recommended by Anderson et al. 1983). Pairs of traps (Hansson 1967, Fryxell et al. 1998) were placed along radii at 15-m intervals (Smith et al. 1975:33), starting 7.5 m from center, out to 97.5 m; this pattern resulting in seven equally-provisioned “rings”, totaling 224 traps (Fig. 1.1). This number of traps was roughly equivalent to that recommended by both Anderson et al. (1983:> 250) and Buckland et al. (1993:> 200). Mark-recapture grids, following common use (e.g., Elkinton et al. 1996), contained 49 live-traps, singly spaced 15 m equidistant in a 7 x 7 square grid with 90-m sides.

We used two web-grid patterns. One pattern had a single trapping web superimposed on three previously established, closely situated mark-recapture grids (Fig. 1.2). This pattern was used in four stands of oak forest. The other pattern had a single web superimposed on a single grid. Using this pattern, 2-3 web-grid pairs were located together, with at least 50 m separating these paired units (Fig. 1.3). This pattern was used in three stands of oak forest.

The software and statistical analyses used for this work are described within the individual chapters addressing the particular objectives of this thesis (see above).

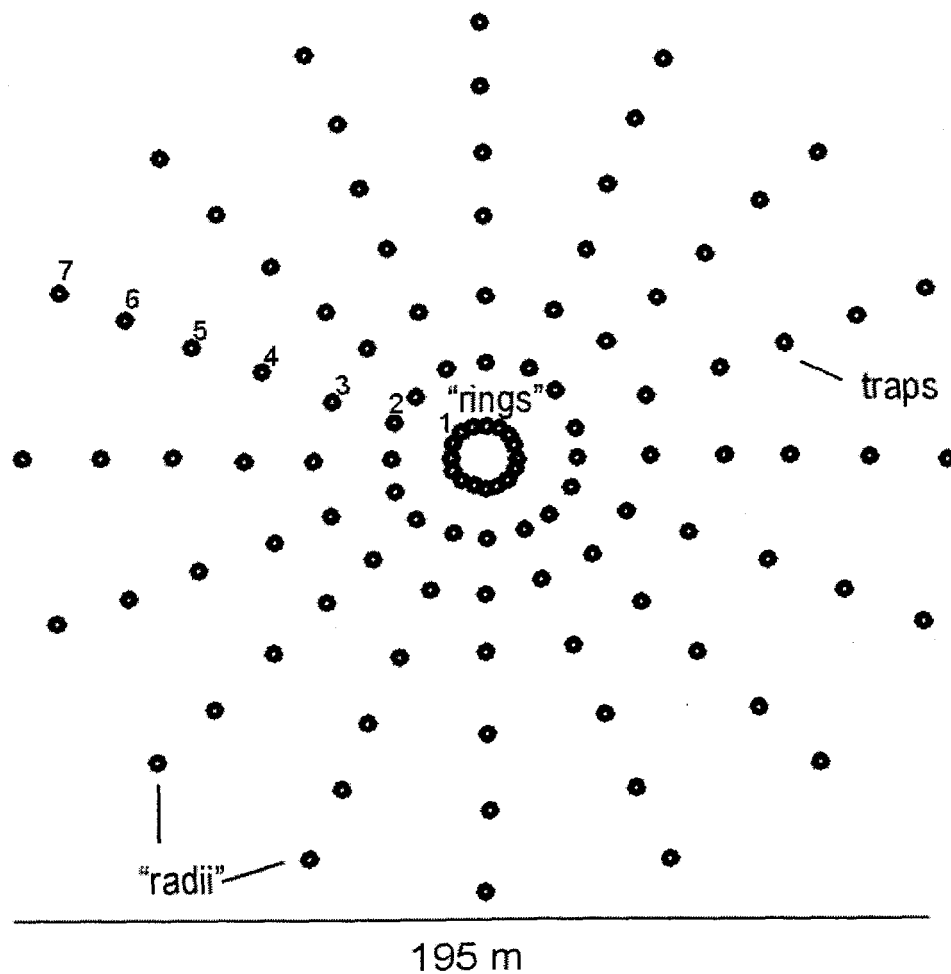


Figure 1.1. Trapping web design most commonly used for trials performed in central Massachusetts between August-December 1996-98. All webs were ca. 3 ha, with 7 "rings of traps. Pairs of live-traps were spaced 15 m along "radii" and the number of "radii" ranged from 6-20; webs with 16 radii were the standard design.

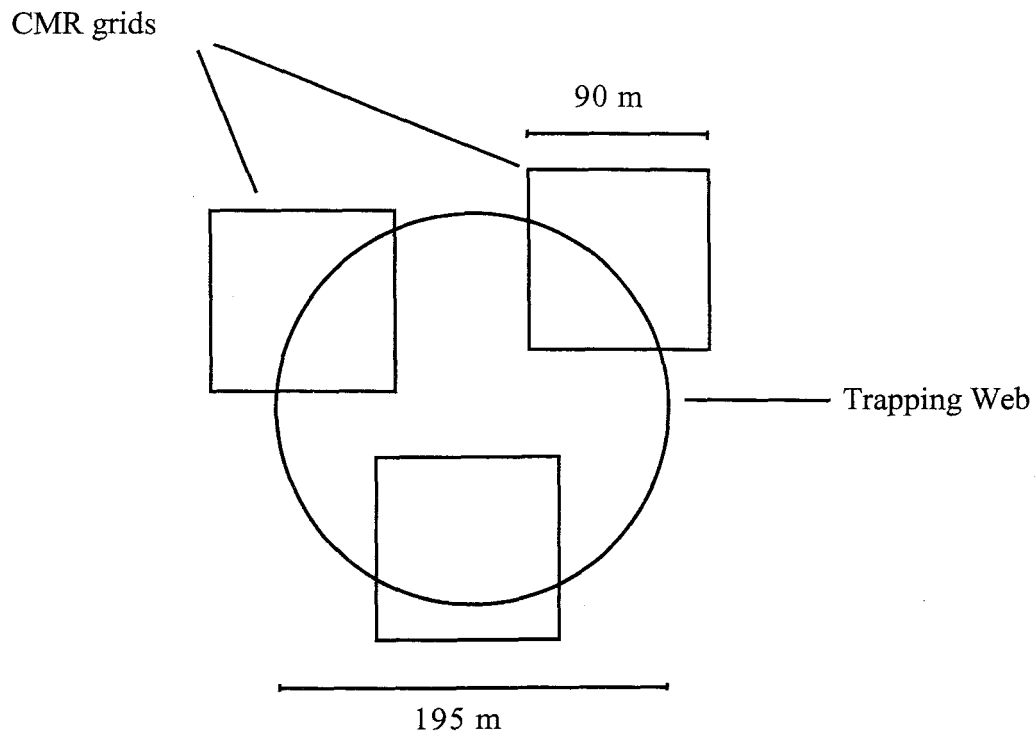


Figure 1.2. Example of placement of single large trapping web in relation to existing mark-recapture trapping grids. (Figures drawn to scale.)

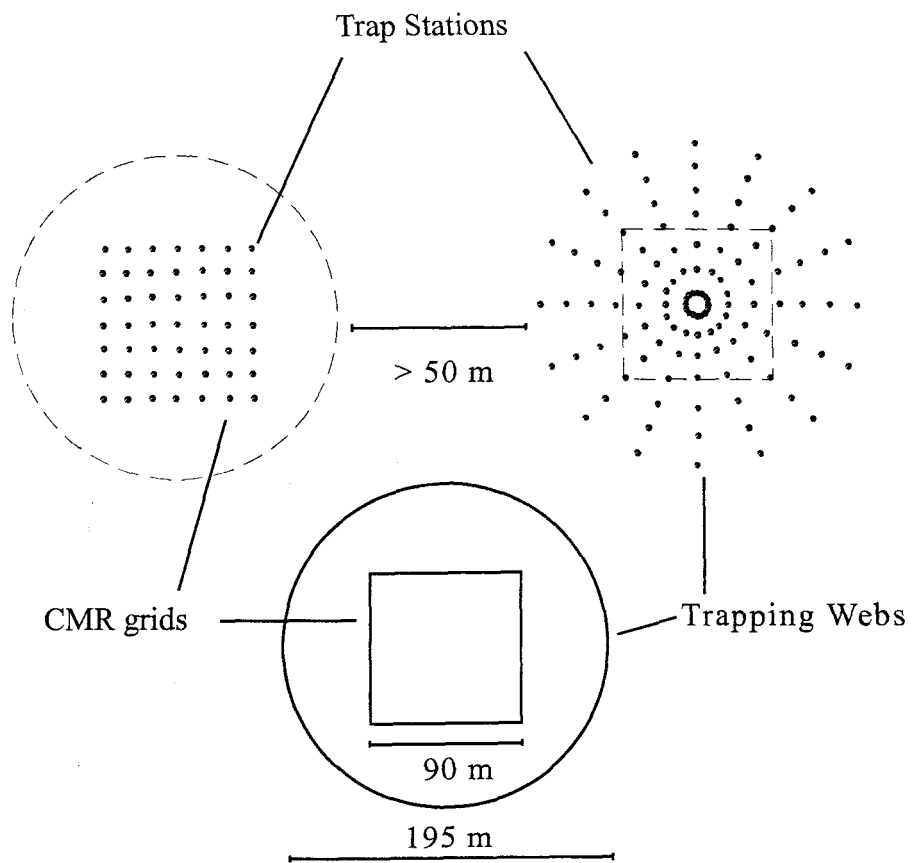


Figure 1.3. Example of placement of trapping webs in relation to paired mark-recapture trapping grids (their contrasting bounds) and trap station layout for both methods. (Figures drawn to scale.)

CHAPTER 2

MOVEMENT: ASSESSMENTS OF EMPIRICAL DATA

Introduction

Movement in space-time remains a little-understood process for most organisms (Turchin 1998). Defined as the process by which “individual organisms are displaced in space over time,” Turchin (1998:3) refers to the population-level consequence of such movement as “population redistribution”—this including dispersal (movement leading to “spatial spread”) and aggregation (movement leading to “population concentration”).

Consideration of such movement by individual animals in a population is integral to the probabilistic estimation of their abundance/density, regardless of the methods used. Closed-population mark-recapture models are based, in part, on the assumption that movements in and out of populations do not occur during repetitive sampling periods, and open-population models that allow immigration and emigration (e.g., Jolly-Seber), do so under the implicit assumption that all emigration is permanent (Pollock et al. 1990:19). (Also, density estimates contrived from mark-recapture abundance estimates often use the mean maximum distance moved [MMDM] by animals captured more than once as a measure of effective trapping area.) Similarly, the trapping web/distance-sampling design, as described by Anderson et al. (1983), is partially based on the assumption that animal movement is “stable”—implying “that there is no directional movement...toward, away from, or through the web during the study; [small mammals] move freely within their home range [and] are not attracted to the center of the trapping grid for any reason.”

It has long been acknowledged, however, that the presence of traps (especially live-traps) affects natural movement of many small mammal species in a complex manner (Getz 1961, Tanaka 1963, Kikkawa 1964, Balph 1968, Gliwicz 1970, Andrzejewski and Rajska 1972, Gurnell 1982, Hurst and Berreen 1985). Live-trapping data may seldom reflect the entire range of natural movement, as captured animals are thwarted until their release; however, observations of increased levels of spatial activity by white-footed mice (*Peromyscus leucopus*) immediately after their release from traps suggest that some home ranges revealed by live-traps may be too large, rather than too small (Sheppe 1967). Correlatively, other studies have observed murid movement to increase with increased grid size (Faust et al. 1971, Bowman et al. 2001a) and trap spacing (Kikkawa 1964, Tew et al. 1994). Nevertheless, the bait used in live-traps (e.g., peanut butter-rolled oats) has been shown to lure mice into trees (Manville et al. 1992), and other mice have been observed to “trap-line” (i.e., follow grid-lines and/or trappers long distances, checking consecutive baited traps) (Stickel 1968 and references therein); this behavior potentially contributing to observations of increased movement by murids. Consequently, movement by even oft-studied small mammals (e.g., peromyscines) is poorly understood, although recent observations have revealed a greater vagility than previously thought (Andrzejewski et al. 2000, Bowman et al. 2001a, Maier 2002).

Also unknown is what potential effects the gradient of trap densities that characterize the trapping web (see Fig. 1.1) may have on small mammal movement. Concentrations of baited traps toward web centers may attract or conceivably repel animals (e.g., the latter due to prolonged human presence/activity and/or the destruction of vegetation/micro-habitat). More simply however, given the vagility of small

mammals, the greater probability of their capture near trapping web centers (Buckland et al. 1993:281), and numerous observations that many small mammals often do not enter the live-trap(s) they encounter for some time (e.g., Hayne 1949, Pearson 1959, Sheppe 1967, Balph 1968, Myton 1974, Hurst and Berreen 1985), both the initial capture and subsequent re-capture of animals may result in their mechanistic “displacement” (*sensu* Turchin 1998) towards trapping web centers, without their being “attracted” per se.

Regardless of mechanism, such inward movement of animals on trapping webs would likely exacerbate “edge-effect” (i.e., capturing animals with ranges overlapping grid edges), limit the duration of sampling trials, negate the use of re-capture data from trapping webs, and potentially result in positively-biased estimates of density.

Accordingly, I evaluated both the net radial movement (to assess displacement) and range of movement of individual, live-trapped white-footed mice (a geographically widespread murid [Lackey et al. 1985]; hereafter “mice”) from empirical trapping web data over mouse age, sex, and a wide range of population densities in an attempt to better understand the function of the trapping web design with its gradient of trap densities.

Methods

Empirical data for mice were obtained from 24 individual trials performed on 12 individual, 3-ha trapping webs located at seven forested sites in central Massachusetts. Trapping webs were deployed between August-December, 1996-98. A single multi-day trial per trapping web per year was considered a unique trial, given that annual mortality for mice usually leads to a complete population turnover (Lackey et al. 1985). In those few cases when webs were trapped twice annually ($n = 7$), only data from one trial (that trial using the most traps) was used to avoid pseudoreplication (Hurlbert 1984).

The net displacement of mice after their initial capture was measured using simple vector quantities that expressed both magnitude and radial direction (i.e., towards either web center or edge). Potential movement by mice during the period from their first trap-encounter to first capture was not examined, because such movement was not discernible from the data. Using the seven, 15 m-spaced concentric rings of this trapping web design (Fig. 1.1; inner-outermost rings as “1-7”) as the basic unit of measure, resultant vectors were derived for individual mice by simply subtracting the number representing the last ring animals were captured in from the number representing the ring of their initial capture; these “resultants,” representing the net radial movement (“NET_MOVE”) of each mouse on a trapping web over a multi-day sampling period, expressed as

$$\overrightarrow{\text{NET_MOVE}} = (\text{ring number})_{\text{initial capture}} - (\text{ring number})_{\text{final capture}} .$$

Thus, mice generated a positive vector quantity if radially displaced towards web centers, a negative vector quantity if displaced towards web edge, or zero net vector quantity; with potential vector quantities ranging from -6 to +6.

The range of movement of individual mice captured more than once was assessed using two different metrics; first using the discrete unit of measurement previously used to assess net radial movement (i.e., the concentric trapping web rings), and then using the maximum omnidirectional distance moved between multiple captures. Both metrics were required to assess the resolution of NET_MOVE, given non-radial movement by mice and the possibility of their radial travel directly across trapping web centers to the same ring (this latter eventuality potentially registering a net movement of zero). As measured

by concentric rings, range of movement values (“RANGE_MOV”) were derived for individual mice by examining sorted multi-capture data and assigning a range, where

$$\text{RANGE_MOV} = (\text{ring number})_{\text{maximum}} - (\text{ring number})_{\text{minimum}}.$$

Thus, mice generated potential positive range values (RANGE_MOV), ranging from 0-6.

Range of movement values (“OMNI_MOV”), as measured by the maximum omnidirectional distance moved between captures, were derived for mice by individually extracting their “maximum distance moved” values from output generated by a program written to trigonometrically calculate all possible distances between sets of capture points on a trapping web (program listed in Appendix 2-A). Input for this program consisted of unique ear-tag numbers identifying individual mice and the coordinates for each of their points of capture, represented by the intersections of a trial’s trapping web radii and rings. Output (all possible distances between capture points per individual mouse for that trial) was manually spot-checked using a Microsoft® EXCEL spreadsheet setup to solve oblique and right triangles using the law of cosines: $a^2 = b^2 + c^2 - 2bc \cos A$.

Statistical Analyses

The potential interactions and simultaneous effects of the trapping web ring (representing trap density), mouse age, and sex on net radial movement (NET_MOVE) were initially assessed using multiway ANOVA (Zar 1996:285). Age and sex were selected as factors because of their widely acknowledged influence on small mammal movement (e.g., Stickel 1968, Holekamp 1984). Gender parity per age (i.e., adult, sub-adult, juvenile) per ring provided the proportional replication required for this ANOVA.

Given the inherent asymmetry of the pooled count data for NET_MOVE over concentric trapping web rings (see Appendix 2-B; innermost and outermost rings generated non-normal count distributions being naturally constrained for certain value categories), these data were graphically examined by pooled ring, transformed as appropriate, and individually analyzed using two-tailed t tests, where $H_0: \mu = \mu_0$.

Single-factor ANOVA was used to assess what effect the population density of white-footed mice may have had on NET_MOVE, RANGE_MOV, and OMNI_MOV. Associated empirical data were also examined to determine what other factors may result in potential differences in these variables.

The effects of mouse age and sex on both RANGE_MOV and OMNI_MOV were evaluated using two-factor ANOVA. The strength of the relationship between these two different range metrics was assessed using correlations, then fit and plotted using JMP IN 3.2.1 (SAS 1997). All other analyses were performed in SYSTAT 10.2.01 (SSI 2002) using a significance level of $P < 0.05$ for all tests.

Results

An ANOVA of the net radial movement of mice on trapping webs (NET_MOVE) revealed no significant interactions between the factors of ring, age, and sex (Table 2.1). The placement of concentric rings' was significant ($P < 0.001$), while the effects of mouse age and sex were not ($P > 0.15$). The number of radii (i.e., number of traps) used for the trapping web had no apparent effect on the net radial movement of mice. Rings 1, 5, 6, and 7 (outermost) exhibited differences from zero net radial movement (Fig. 2.1); the weighted mean of NET_MOVE (weighted in proportion to the respective number of mice per ring) was 0.147 (95% CI: 0.100, 0.194), indicating a general net radial

movement towards trapping web centers. Examination of the factor interactions indicated that male mice generally exhibited only slightly more net movement than female mice, with the most discernible differences existing between the more numerous male and female adults in outermost rings (Fig. 2.2).

Further examination of the asymmetrical pooled count data for NET_MOVE (Appendix 2-B) led to the truncation of both rings 1 and 7 for final consideration of this movement, resulting in the decline of the weighted mean of NET_MOVE to 0.076 (95% CI: 0.018, 0.134); this still indicating an overall movement towards trapping web centers. Examination of probability plots for rings 5 and 6 led to the logarithmic transformation ($x' = \ln[x + 2]$) of only ring 6 NET_MOVE values, whereupon NET_MOVE for pooled ring 6 was no longer significant ($t = 1.197$, $df = 272$, $P = 0.232$; where $H_0: \mu = \mu_{0.693}$); pooled ring 5 remained significant ($t = 2.120$, $df = 277$, $P = 0.035$; where $H_0: \mu = \mu_0$).

Population density's effect on NET_MOVE values was not significant in an ANOVA ($F = 1.385$, $df = 21$, $P = 0.114$), but a trend did appear to exist in which net movement decreased with increased density on trapping webs (Fig. 2.3). Individual trials exhibiting positive net movement towards trapping web centers occurred throughout the range of population densities sampled (range: 2-123 mice/ha), with no trials exhibiting net movement away from web centers. Examination of associated empirical data failed to reveal any consistent differences (e.g., time of year, sympatric murid species) between individual trials exhibiting significant and non-significant movement, other than variation in ring category counts; this, considerable at times, even between immediately adjacent webs trapped simultaneously (e.g., Fig 2.4).

ANOVAs of both range-of-movement metrics (RANGE_MOV, OMNI_MOV) revealed no significant interactions between the factors of mouse age and sex (Table 2.2), while factor effects were significant for both metrics (AGE: $P < 0.001$; SEX: $P < 0.02$); where adult mice moved further than sub-adult mice, which moved further than juvenile mice; and male mice moved further than female mice as measured by both metrics.

Population density had significant effect on both RANGE_MOV ($F = 8.130$, $df = 21$, $P < 0.001$) and OMNI_MOV ($F = 15.990$, $df = 20$, $P < 0.001$) values, with both metrics decreasing similarly with increased density (Fig. 2.5). Although a strong positive relationship existed between these metrics ($r^2_{\text{Pearson, pair-wise}} = 0.78$; Fig. 2.6), OMNI_MOV provided a higher resolution than RANGE_MOV for such movement (see Figs. 2.5, 2.6).

Further graphical examination of OMNI_MOV data by quantile plot (Fig. 2.7) and pooled trapping ring (Fig. 2.8)—prompted by deviation in the “rate of change” of both range metrics at a population density of ca. 18 mice/ha (see Fig. 2.5) and this studies’ use of 15-m trap-spacing on all radii—revealed modes at 0 m, 15 m, and 30 m; movements of these distances, representing 57% of all OMNI_MOV values ($N = 1608$), made by mice increasingly towards outermost trapping web rings (see Fig. 2.8).

Allowing that the remaining OMNI_MOV values ($N = 695$; Fig. 2.9) better represent potential natural movement by mice than movements of 0, 15, and 30 m (based on the extreme unlikelihood that any mice would move zero distance—as more than 27% of the re-captured mice in this study purportedly did), another ANOVA was performed to assess the effect of population density after disregarding the 0-m, 15-m, and 30-m values. This analysis revealed greater mean movement at all levels of population density (Figs. 2.10 vs. 2.5), and greater coherency of results; these data, perhaps best described as

$$\ln(\text{OMNI_MOVE}) = 4.34478 - 0.26061 \ln(\text{WEB_DEN}),$$

exhibited substantial omnidirectional movement (albeit still trap-mediated) by white-footed mice within all population densities sampled using trapping webs (Fig. 2.11).

Discussion

The trapping web/distance-sampling design described by Anderson et al. (1983) requires that animal movement remain stable (i.e., that no directional movement occur during the study—specifically, that there be no attraction to grid center for any reason). The gradient of trap densities integral to this design, however, may itself mechanistically displace animals toward higher trap densities near web centers without “attracting” them per se. Examination of empirical trapping web data using a simple net-movement metric (NET_MOVE) revealed a modicum of movement (“displacement”) toward web centers by white-footed mice. Such radial movement was observed to have occurred throughout trapping webs (i.e., originated in all rings, except the innermost; e.g., Fig. 2.4), but was statistically significant only in outermost rings of greater area containing more mice.

Was such inward movement biologically significant in individual trapping trials? Comparisons between the range-of-movement metrics RANGE_MOV (using the same concentric web rings as NET_MOVE) and OMNI_MOVE (using the maximum distance mice moved between multiple captures) indicated that the former metric was of lower resolution (see Figs. 2.5, 2.6); thus, NET_MOVE was also conservative and less likely to portray the actual extent of inward movement on trapping webs by white-footed mice. Moreover, only a few cases of such inward movement (these statistically “insignificant” as defined by this study’s analyses) near trapping web centers may greatly affect resultant

point estimates given the critical nature of such areas (see Buckland et al. 1993:348). Given that only first-capture trapping web data are generally used in the estimation of density (Buckland et al. 1993:278), such movement over a multi-day sampling period may seem to only negate the use of recapture data (another use suggested by Anderson et al. [1983] and used by others [e.g., Corn and Conroy 1998]). Nevertheless, given that small mammals often do not enter the live-traps they encounter for some time, it is reasonable to assume that movement prior to first-capture may similarly be affected by the greater probability of capture in trapping web areas with higher trap densities. Thus, any discernible displacement of animals toward trapping web centers is of concern and mandates the assessment of such aggregate movement during trapping sessions.

Conceivably, concentrations of baited traps near web centers may have been accountable for inward movement by mice. Nevertheless, overt movement toward a concentrated food source (the many baited traps at web center) would resemble a melee, rather than the categorically-defined movement exhibited by mice in this study: in which, adult mice ranged further than sub-adult mice, which ranged further than juvenile mice, and male mice ranged further than female mice. Additionally, accounts of attraction to bait (see above) do not indicate *Peromyscus* mice left their normal ranges (Stickel 1948); as such, movement across 3-ha trapping webs unlikely during typical 4- to 5-day trials, except at low population densities, given the existence of social fences (Hestbeck 1982).

The mechanism by which displacement towards trapping web centers occurs is likely dependant on the relationship between trap spacing along web radii, and animals' home-range size and/or tendency to wander, as alluded to by Buckland et al. (1993:281). In other words, displacement is likely contingent on exposure to a trap-density gradient

(in this study, the gradient was defined by the 15 m-spaced concentric web rings), and its amelioration dependant on trap spacing appropriate to the species being studied, the variability in their movement, their population density, and the sampled sites' habitats. Unfortunately, there have been few guidelines available for determining trap spacing in relation to average home range size or mean distance moved (Buckland et al. 1993:281).

Paradoxically, the gradient of trap densities provided by the trapping web design might itself prove useful in elucidating optimal trap spacing, given the amplitude of available distances between live-traps. Examination of this study's pooled data (Figs. 2.7, 2.8) revealed that movements of 0 m, 15 m, and 30 m could be disregarded in the final assessment of movement, given the dual unlikelihood that animals would actually move zero distance, and that movements of 15 m and 30 m, increasingly predominate in the outermost trapping web rings (Fig. 2.8), represented "natural" movement. Remaining movement values (43% of all OMNI_MOV values, $N = 695$) were normally distributed (disregarding scattered values over 50 m; see Fig. 2.9), and when assessed by population density (Fig. 2.10), provided a coherent pattern of movement by white-footed mice on 3-ha trapping webs over a wide range of population densities in forested habitat (Fig. 2.11).

Large numbers of mice moved considerable distances across 3-ha trapping webs, such movement exposing individual mice to a gradient of trap densities, and likely accounting for their displacement toward web centers. The mean maximum distances moved (OMNI_MOV) by these mice ranged from 77.9 m (median, 74.9 m) to 24.6 m (median, 22.9 m) (lowest-to-highest population densities, based on analysis illustrated by Fig. 2.10). Other non-dispersing white-footed mice have been observed to move very similar ranges of distance within their home landscapes (e.g., Sheppe 1967, Wegner and

Merriam 1990), as have deer mice (*Peromyscus maniculatus*) (e.g., Bowman et al. 2001a), cotton mice (*Peromyscus gossypinus*) (e.g., Faust et al. 1971), golden mice (*Ochrotomys nuttalli*) (e.g., Faust et al. 1971), and wood mice (*Apodemus sylvaticus*) (e.g., Chitty 1937, Kikkawa 1964, Tew et al. 1994). Allowing regularity of such movement by these mice, even for a portion of a sampled population, the 15-m trap-spacing interval along web radii appears insufficient to prevent the displacement of peromyscines and similar murids toward trapping web centers.

This study's use of 15-m trap spacing was based on convention; its use considered "a good compromise for most of the common [small mammal] species studied throughout the world" (Smith et al. 1975), its widespread employment for transects and rectangular grids revealed by a recent review of 127 murid trapping studies (Bowman et al. 2001b). It is widely acknowledged, however, that population density affects small mammal movement (see this study; Figs. 2.10, 2.11), and perhaps, as stated by Tew et al. (1994), "...there can be no *a priori* recommendation for [optimal] trap spacing [because] population density and motility... will vary between species and habitats." Nevertheless, optimal trap spacing may be more critical to the successful operation of rectangular trapping grids, than to that of trapping webs. For example, on rectangular grids, spacing dictates perceived range (prompting the recommendation that traps be set "...sufficiently close for resident individuals to be caught in at least two traps and sufficiently distant for the whole range to be demonstrated without excessive numbers of captures" [see Kikkawa 1964]), which, in turn, is used to determine the effective trapping area for the estimation of population density. On trapping webs, however, it appears that trap spacing need only be great enough to prevent the displacement of individuals toward web centers.

As such, (keeping in mind that the movements described here [e.g., Figs. 2.7-2.11] were omni-directional and not just radial in nature) this study's results suggest that an *a priori* trap spacing along web radii of as little as 20-30 m may be sufficient to prevent most displacement of white-footed mice and murids of similar disposition toward trapping web centers in similar habitat, except at low densities (ca. 10 or fewer mice/ha; see Fig. 2.11).

This study's intent was not to establish appropriate trap spacing for trapping webs (and it is important that these results not be interpreted as any but the most preliminary); yet, trap spacing may prove almost as crucial to this methodology's use as for transect and rectangular-grid trapping methodologies. As stated by Buckland et al. (1993:281), "The challenge with the trapping web is to collect data that mimic the assumptions of point transect sampling and analysis theory. In particular, trap spacing must be related to average home range size or average distance moved and there are presently few guidelines for this decision. [continuing] If the animals tend to move in home ranges that are small relative to the size of the web and the trap spacing, then the trapping web may perform well." As further caveat regarding this study's results, all observed distances were derived via live-traps, and as noted by Chitty (1937; referring to a trap spacing of ca. 4.6 m used for wood mice), "Movements within a close-spaced grid give no indication of the extent of natural wanderings." Nevertheless, movements indicated by this study's final results match the dimensions of the average home range size for white-footed mice given by Lackey et al. (1985: 0.1 ha): in this study (see Fig. 2.9), the mean of all mean maximum distances moved was 35.1 m (median, 31.8 m); whereas the diameter of a 0.1-ha circular range is 35.7 m and the side of a square range is 31.6 m. Thus, it is unlikely that the movement observed in this study was wholly an artifact of

trap spacing, if we accept the veracity of prior observations. If further investigation of the trapping web design reveals that web-derived small mammal movement is representative of natural movement, this methodology may provide a long-sought, empirically-defined trap-spacing index for the trapping web and other methodologies, specific to small mammal species in their specific habitats.

In summary, the movement of animals remains a critical but little understood process affecting the assessment of their population numbers. Often further complicating such assessments are the methods by which researchers evaluate their species of interest. The trapping web/distance sampling design requires that animal movement remain stable; however, in this study I have shown how the gradient of trap densities that characterizes trapping webs may affect the movement of white-footed mice and other small mammals by displacing them toward web centers over time. Such movement, itself, would likely only exacerbate edge-effect in outermost web rings, limit trial periods, and negate the use of recapture data from trapping webs. Nevertheless, given the likelihood that movement prior to a small mammal's delayed first capture would similarly be affected, such aggregative movement could also lead to positively biased estimates of density (such bias most graphically exhibited by frequency "spikes" within innermost trapping web rings, such as those often demonstrated in Chapter 3). Thus, those using trapping webs should assess their data for such inward movement (e.g., Parmenter et al. 2003).

Given the considerable distances that many white-footed mice were observed to move over trapping webs in this study, the 15-m trap spacing used along radii appeared insufficient to prevent the displacement of mice toward web centers, suggesting use of increased trap spacings of 20-30 m. Nonetheless, how trap spacing relates to the

distances moved by animals remains unknown and further investigation of the trapping web is required. For example, in this study, traps were checked along web radii, except for the innermost ring, which was checked along its circumference. Mice, however, may have followed our paths along outer radii (see above), thus exacerbating radial movement between concentric web rings. Further study might assess such behavior by animals such as murids on trapping webs by comparing radial movement between traps checked along radii versus those checked around the circumference of each concentric web ring.

Finally, given the amplitude of available distances between traps supplied by the gradient of trap densities constituting the trapping web, this trap layout design may prove useful in elucidating optimal trap spacing; as such, providing a long-sought, empirically-defined trap-spacing index for use with this method, as well as other trapping methods, specific to small mammal species at various population densities in specific habitats.

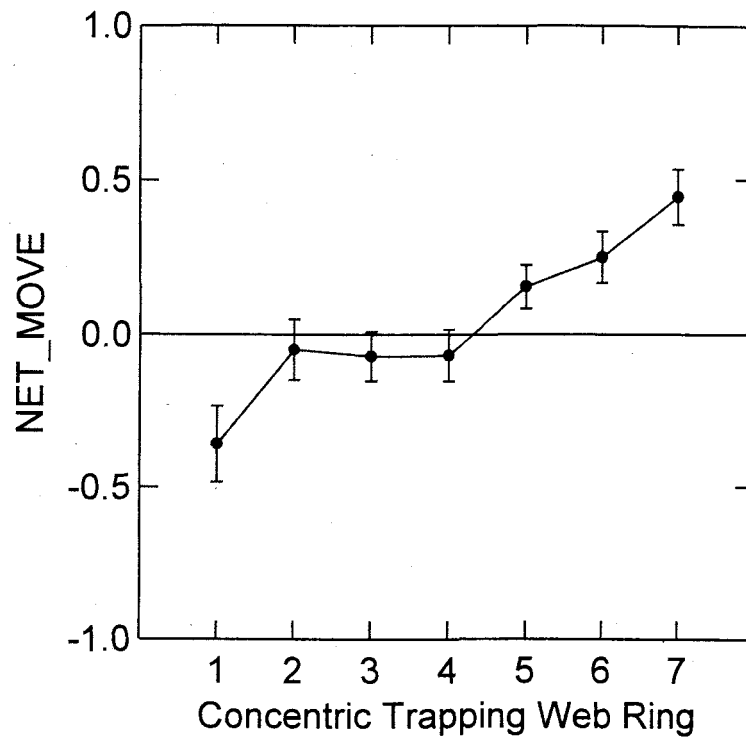


Figure 2.1. Least-squares-means (ANOVA) and standard errors of net radial movement (NET_MOVE) by white-footed mice (*Peromyscus leucopus*) over concentric rings during 24 trapping web trials performed in Massachusetts between August-December, 1996-98.

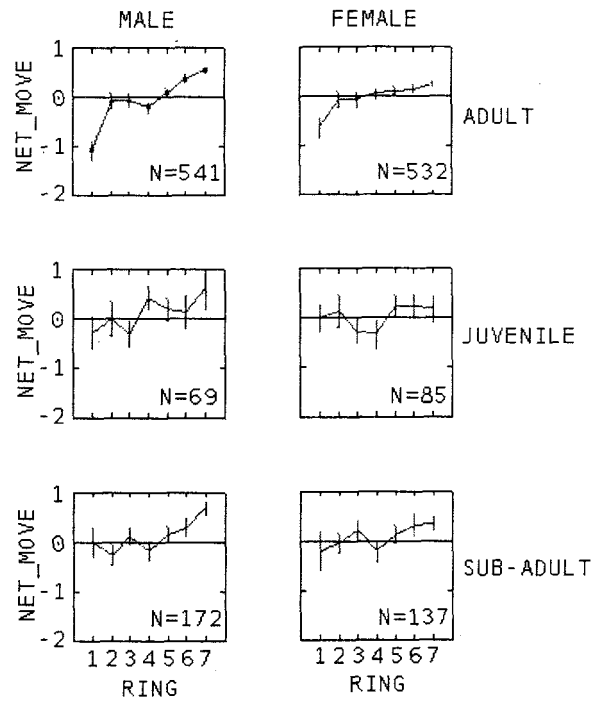


Figure 2.2. Least-squares-means with standard errors (ANOVA) of net radial movement (NET_MOVE) and interactions with concentric trapping web rings, mouse age, and sex.

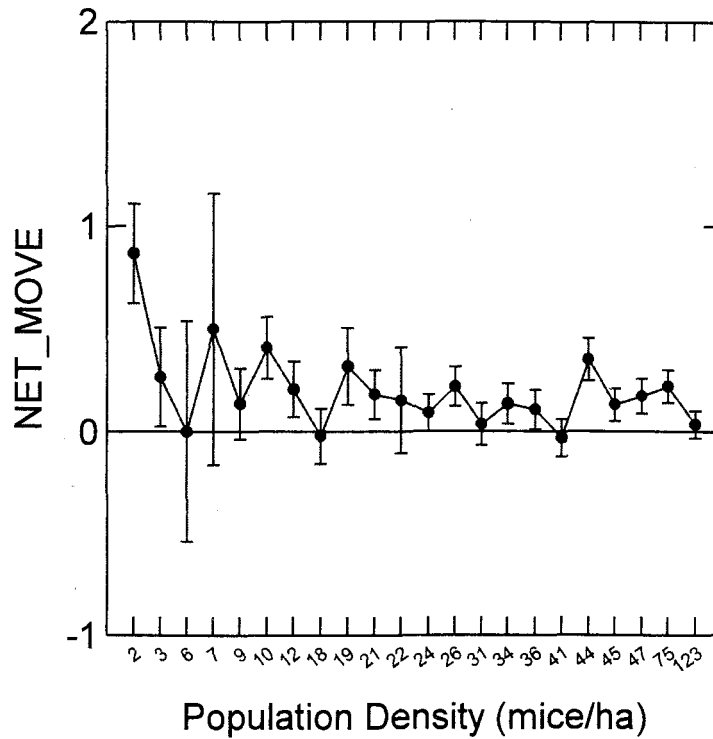


Figure 2.3. Least-squares-means with standard errors (ANOVA) of net radial movement (NET_MOVE) over a wide range of population densities (2-123 mice/ha) of white-footed mice sampled throughout central Massachusetts between August-December, 1996-98.

Figure 2.4. Example of variation in ring category counts between simultaneously trapped, immediately adjacent trapping webs exhibiting significant and non-significant net radial movement (NET_MOVE) towards their centers. “Web1se98” (left) exhibited positive radial net movement towards its center ($P = 0.01$) with 212 white-footed mice, while “Web2se98” (right), with 293 white-footed mice, did not ($P = 0.447$).

Figure 2.4

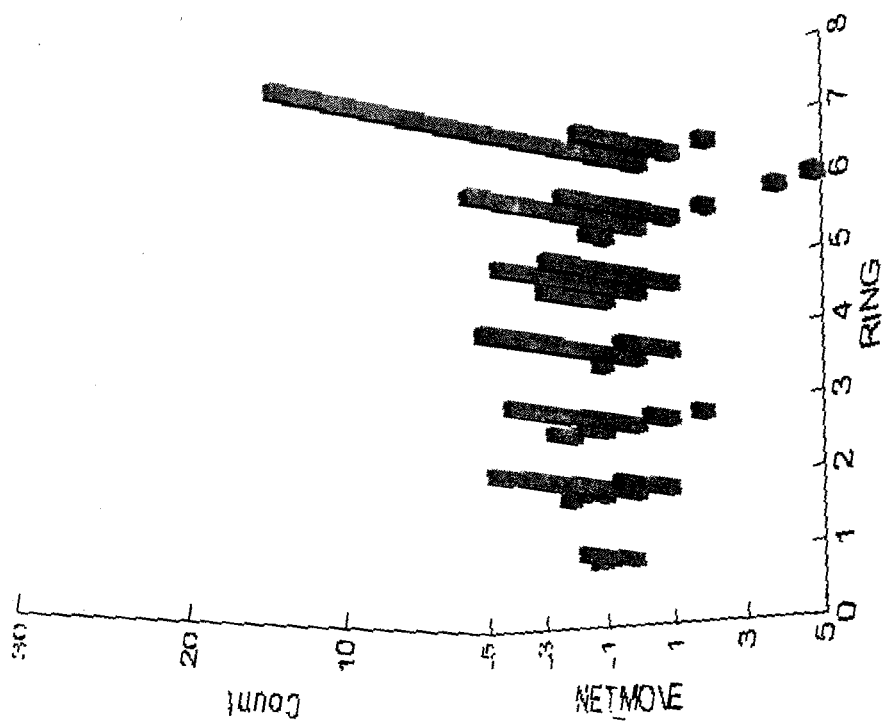
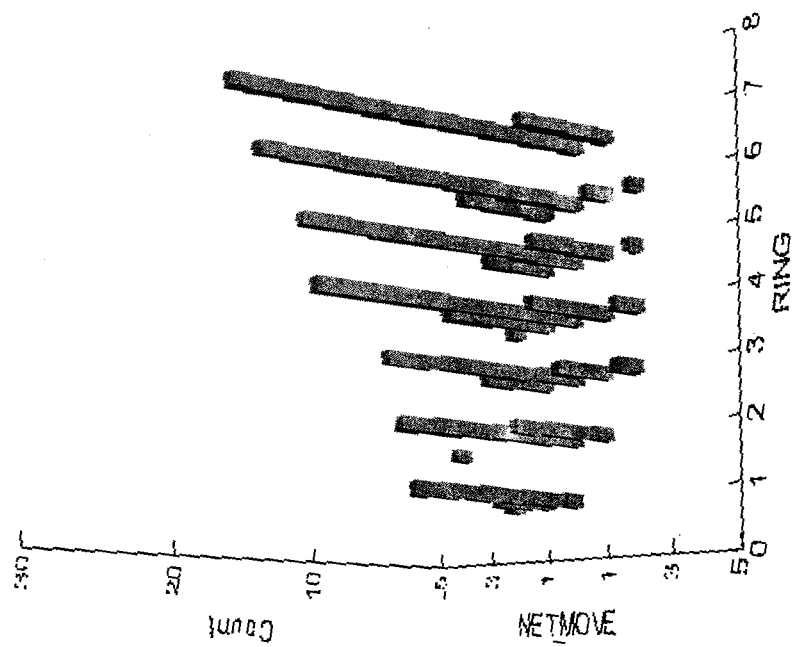


Figure 2.5. Least-squares-means with standard errors (ANOVA) of range of movement of white-footed mice as measured by concentric trapping web rings (RANGE_MOV) and omni-directionally (OMNI_MOV) over population density.

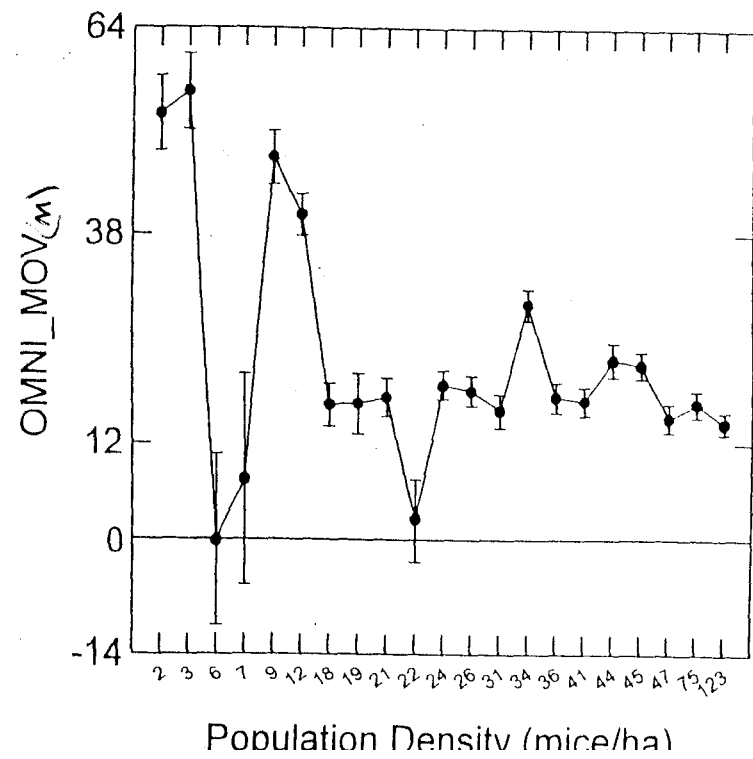
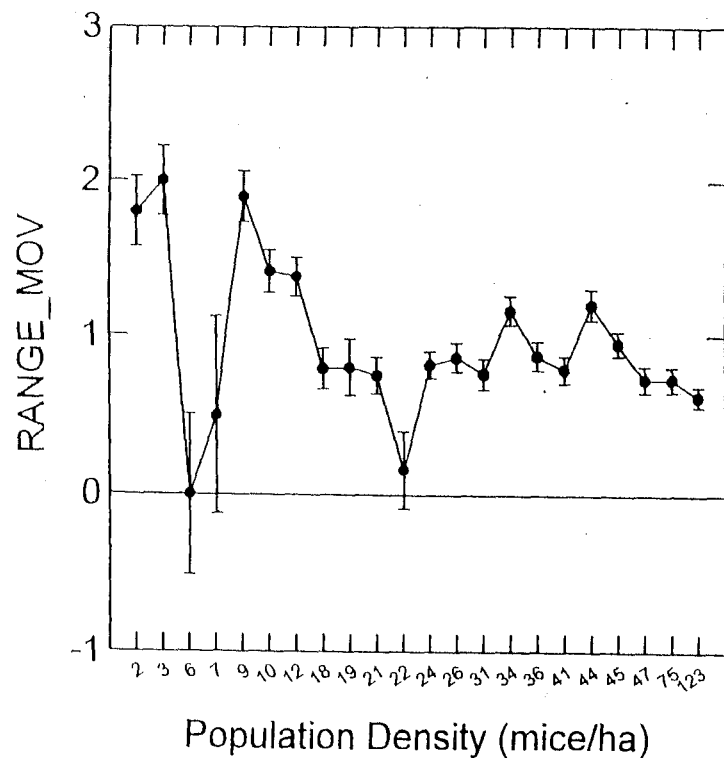
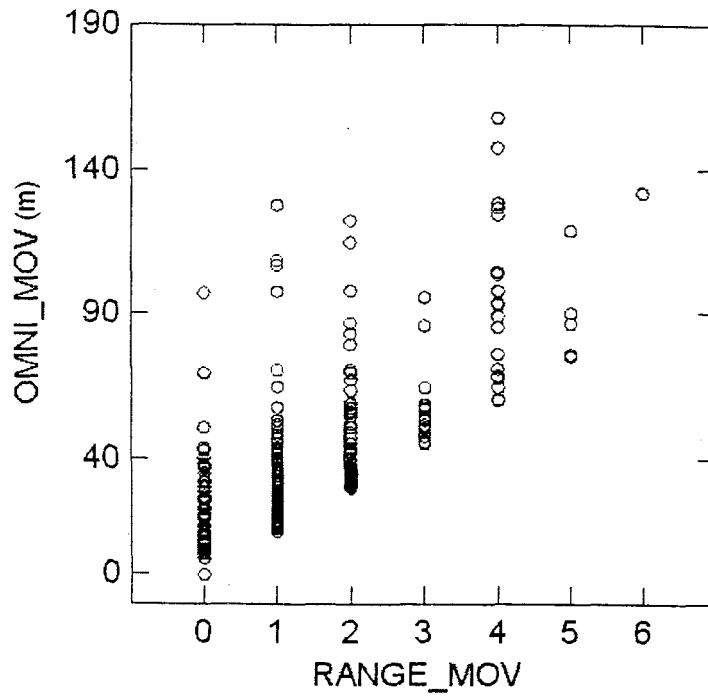


Figure 2.5



. RANGE_MOV vs. OMNI_MOV; latter metric shows higher resolution.

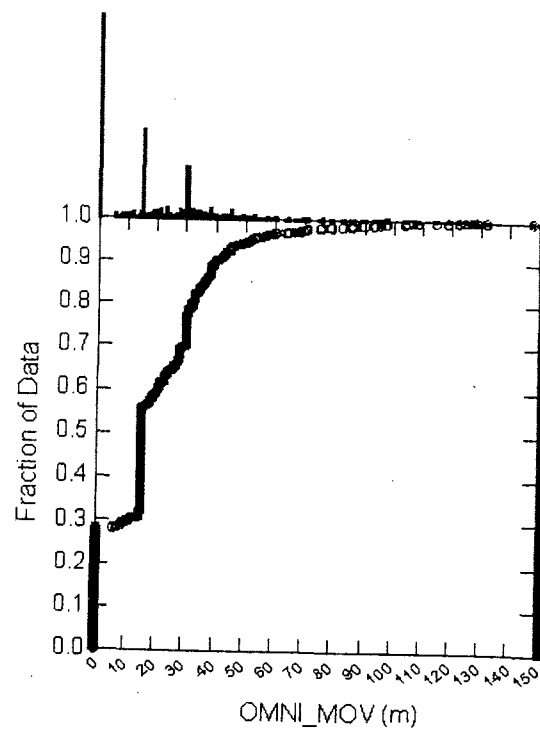


Figure 2.7. Quantile plot of OMNI_MOV displaying modes of 0-m, 15-m, and 30-m; these values represent 57% of all OMNI_MOV values ($N = 1608$).

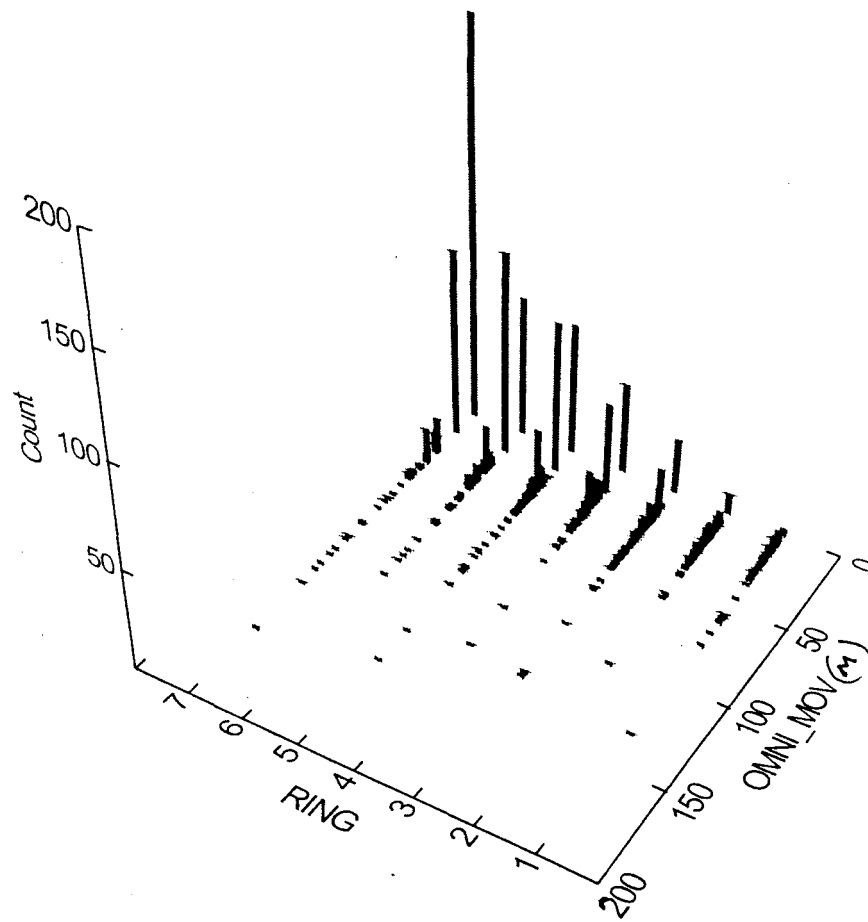


Figure 2.8. Three-dimensional plot of OMNI_MOV displaying the increasing prevalence of distance values 0-m, 15-m, and 30-m in outer trapping web rings.

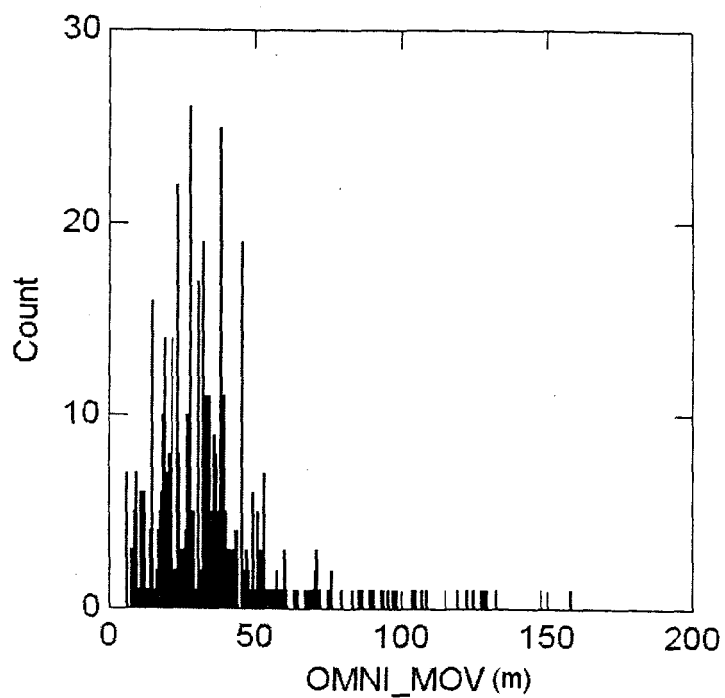


Figure 2.9. Distribution of remaining OMNI_MOV values ($N = 695$) after 0-m, 15-m, and 30-m distances disregarded. Further disregarding movements over 50 m, yields a highly normal distribution.

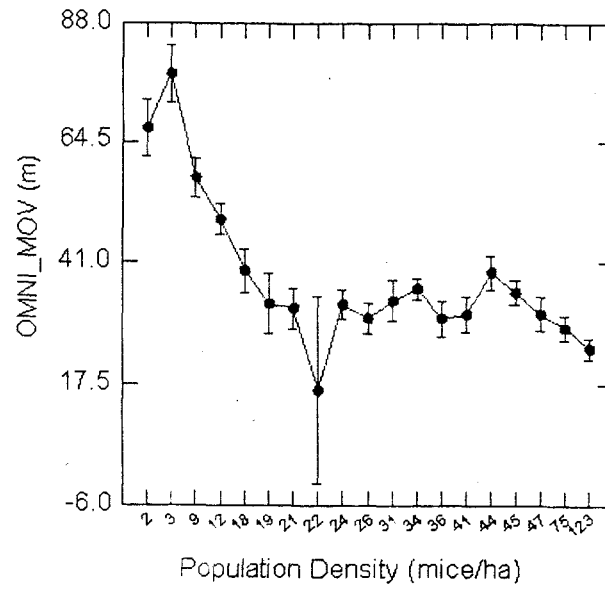


Figure 2.10. Least-squares-means with standard errors (ANOVA) of OMNI_MOV, disregarding movements of 0-m, 15-m, and 30-m by mice.

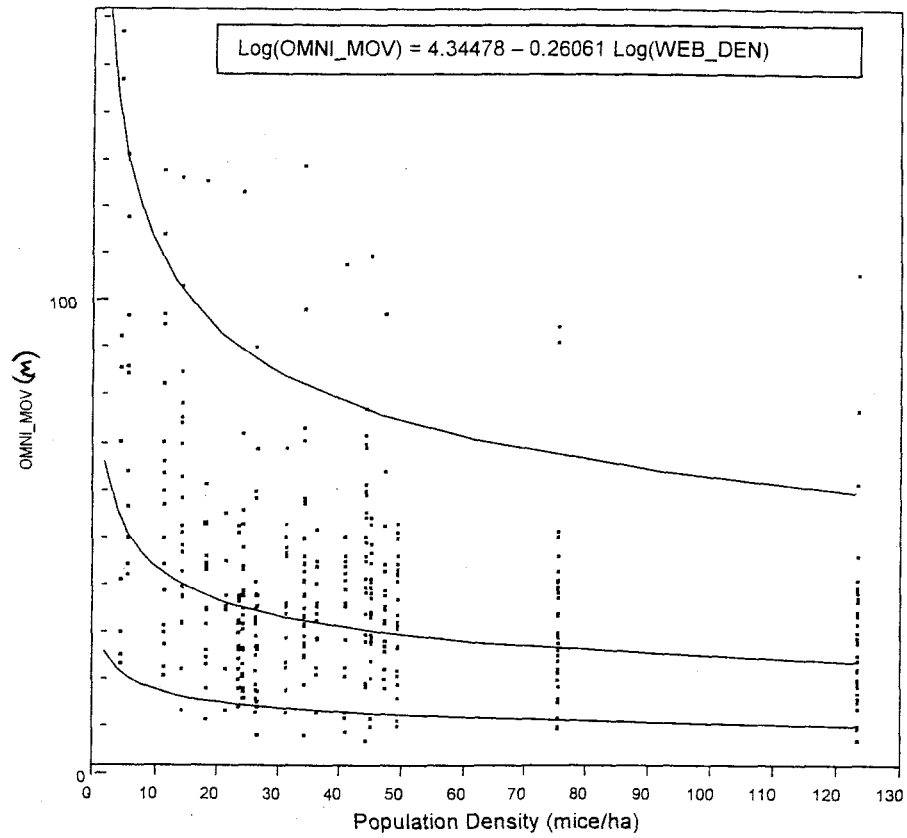


Figure 2.11. Omni-directional movement (OMNI_MOV) of white-footed mice across 3-ha trapping webs over a range of population densities after disregarding movements of 0-m, 15-m, and 30-m. Movement by mice at high densities is greater than expected.

Table 2.1. Multiway ANOVA comparing the simultaneous effects of concentric ring, mouse age, and sex on net radial movement by white-footed mice (*Peromyscus leucopus*) during 24 trapping web trials performed throughout central Massachusetts between August-December, 1996-1998.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
RING ^a	34.404	6	5.734	7.004	< 0.01
AGE ^b	3.153	2	1.577	1.926	0.15
SEX	0.143	1	0.143	0.175	0.68
RING*AGE	13.029	12	1.086	1.326	0.20
RING*SEX	4.386	6		0.893	0.50
AGE*SEX	0.411	2	0.206	0.251	0.78
RING*AGE*SEX	7.045	12	0.587	0.717	0.74
Error	1223.093	1494	0.819		

^a Concentric trapping web rings (1-7), spaced 15 m equidistant.

^b Adult, sub-adult, and juvenile.

CHAPTER 3

HETEROGENEITY: ASSESSMENTS OF EFFECT AND METHOD

Introduction

Variation in the probability of capture among animals, generally referred to as “heterogeneity”, has been reported for numerous species, including various *Peromyscus* mice and *Clethrionomys* voles (Young et al. 1952, Davis and Emlen 1956, Pearson 1959, Tanaka 1963, Sheppe 1967, Balph 1968, Gliwicz 1970, Watts 1970, Summerlin and Wolfe 1973, Mihok 1979, Gurnell 1982, Hurst and Berreen 1985). Induced by factors such as species, sex, age, social dominance, innate level of activity, trap type, the number of traps (trap density), and habitat differences (Kikkawa 1964), heterogeneity has been shown to cause substantial negative bias in the estimation of population parameters (White et al. 1982:63). Thus, knowledge of various capture-probability models and their assumptions is required to use mark-recapture and removal methods.

In contrast, the trapping web design, as presented by Anderson et al. (1983), neither entails specific assumptions regarding heterogeneity nor requires knowledge of capture probability models; generalizing, the authors “envision the population under Model M_{tbh} : capture probability varying with time, behavior, and capture heterogeneity.” In other words, most sources of heterogeneity are considered to contribute little to bias, provided all animals of interest are detected at trapping-web center (Thomas et al. 2002). In yet other words, “the specific reasons why an object was not detected are unimportant” (Buckland et al. 1993:23). Given that only first-captures are usually used for density

estimation, it is readily apparent how variation in capture probability due to either time or behavioral trap response (i.e., “trap-happy” or “trap-shy” animals) is lessened, if not completely eliminated (Buckland et al. 1993:278). Nevertheless, it is unclear why capture heterogeneity may be considered “unimportant” in the use of the trapping web.

Heterogeneity in other types of distance sampling data is commonly dealt with by stratification or the use of covariates in analysis (Buckland et al. 1993:99); however, a search of the literature regarding the trapping web produced no records of such efforts with empirical trapping web data, and few articles regarding the effects of heterogeneity on density estimates derived from similar data (e.g., Ramsey et al. 1987). Effective use of the trapping web would seem contingent on the recognition of heterogeneity and any potential effect. Accordingly, in this study, I first evaluate heterogeneity by sex and age in trapping web data representing a wide range of population densities for two, geographically-widespread woodland murids, white-footed mice (*Peromyscus leucopus*, hereafter “mice”) and southern red-backed voles (*Clethrionomys gapperi*, hereafter “voles”); I then assess what effect such heterogeneity may have on density estimates and discuss aspects of trapping web methodology/analysis highlighted by the empirical data.

Methods

First-capture data for mice and voles were obtained from 12 individual, 3-ha trapping webs located at seven forested sites throughout central Massachusetts. These trapping webs were live-trapped between August-December, 1996-98, yielding 24 trials for mice (Appendices 3-A [sex], 3-C [age]) and 23 trials for voles (Appendices 3-B [sex], 3-D [age]). A single multi-day trial per trapping web per year was considered a replicate sample, given that annual mortality for both murid species usually leads to a complete

population turnover (Merritt 1981, Lackey et al. 1985). In those few cases when webs were trapped twice annually ($n = 7$), only data from one of the trials (that trial using the greatest number of traps) was used to prevent pseudoreplication (Hurlbert 1984).

The linear quantitative sequence of area per concentric ring provided by the trapping web design used in this study (Fig. 1.1) aptly allowed evaluation of linear trend (in this case, “heterogeneity”) among sequential ring proportions—a more powerful procedure than the hypothesis test of difference among proportions (Zar 1996:562). Performed in SAS (SAS Institute 1999) and based upon the regression coefficient for the weighted linear regression of the binomial proportions on the scores of the levels of the explanatory variable, the Cochran-Armitage test for trend (PROC FREQ) was applied to 2×7 contingency tables. In these tables, the explanatory variable was the sequential web ring (i.e., “1-7”; an ordinal variable representing a trap-density gradient level) and the separately evaluated, two-level character (“response”) variables were either sex or age for each murid species. Mice and voles were grouped as either “adult” or “juvenile” (the latter classification including both juvenile and sub-adult individuals for mice). The null hypothesis for these tests was “no trend” (i.e., no significant heterogeneity, the binomial proportion $p_{i1} = n_{i1}/n_i$ was the same for all levels [rings] of the explanatory variable).

Initial trend tests for heterogeneity pooled replicate samples (listed as individual trapping web trials in Appendices 3-A to -D) per species by sex and age, based on the assumption that such samples were homogenous (i.e., that all samples came from the same “population”, in that the individuals of a species would generally exhibit species-specific behavior). When these two-tailed pooled tests displayed a trend, their component trials (the “samples”) were individually analyzed using one-tailed trend tests.

To assess the potential effect of heterogeneity on trapping web density estimates, relationships between density estimates of individual heterogeneous trials and their paired null-heterogeneous models (i.e., with $p_{i1} = n_{i1}/n_i$ equivalent for all rings) were evaluated using concordance correlation (Lin 1989, Zar 1996:401); the coefficient

$$r_c = \frac{2 \sum xy}{\sum x^2 + \sum y^2 + (n-1)(\bar{X} - \bar{Y})^2},$$

providing a superior index of the agreement between two estimates (or readings) from the same sample by measuring variation from a 45° line through the origin (the “concordance line”). Lin (1989) confirmed this technique to be robust with samples as small as $n = 10$. Null-heterogeneous models were developed from individual heterogeneous trials by amending the binomial proportions of a trapping web’s rings to approximate the pooled capture frequencies of the two (or, if necessary, three) innermost rings, this source or “seed” proportion referred to as the “pooled innermost proportion”, expressed as

$$\text{PIP}_{(\text{non-affected sub-population})} = \frac{\sum (\text{non-affected sub-population, rings.1+2})}{\sum (\text{total captured, rings.1+2})}.$$

For example, if two of seven mice captured in ring 1 and 10 of 23 mice captured in ring 2 were adults ($\text{PIP}_{\text{adults}} = 0.40$), the appropriate number of juvenile mice were either added (or occasionally subtracted) from rings 2-7 to match the PIP as closely as possible; making the binomial proportion $p_{i1} = n_{i1}/n_i$ essentially equivalent for all rings (Fig. 3.1).

Proportions of the innermost ring (ring 1) were never altered, under the assumption that they best-represented “truth” ($f[x]$); and proportions of inner trapping web rings sampling lower animal densities that included zero were not amended due to the intractability of cell fractions in binomial analyses. All density estimates were generated using program DISTANCE (Thomas et al. 1998). A significance level of $P < 0.05$ was used for all tests.

Results

Neither murid species exhibited sex-induced heterogeneity in the initial pooled tests (trend test: [mice] $\chi^2 = 0.175$, $df = 1$, $P > 0.6$; [voles] $\chi^2 = 0.001$, $df = 1$, $P > 0.9$); whereas both species exhibited age-induced heterogeneity among adults and juveniles (trend test: [mice] $\chi^2 = 44.144$, $df = 1$, $P < 0.001$; [voles] $\chi^2 = 15.092$, $df = 1$, $P < 0.001$), with pooled proportions of juveniles declining significantly from inner to outer trapping web rings (Fig. 3.2). Interspecific differences in capture probability existed; pooled juvenile voles exhibited smaller capture probability ratios (range: 0.097-0.278) than pooled juvenile mice (range: 0.262-0.477) (two-tailed t test: $t = 4.54$, $df = 12$, $P < 0.001$).

Twenty-eight percent of the individual age trials (mice trials = 10, vole trials = 3) exhibited juvenile proportions declining significantly from inner to outer rings, with other trials marginally exhibiting (i.e., $0.05 < P < 0.10$) the same form of heterogeneity. Reverse trend (i.e., juvenile proportions increasing towards outer rings) was marginally exhibited by a few trials that measured very low population densities. Individual trials exhibited age-induced heterogeneity over a wide range of densities (8.65-149.36/ha).

Heterogeneity induced by age was not observed to have an effect on the trapping web density estimates of these murids (Fig. 3.3), whether trapping web data were post-stratified or not (Table 3.1). Concordant estimates were reproduced between individual

heterogeneous trials and their paired null-heterogeneous models (concordance: $r_c = 0.974$; 95% CI: $L_1 = 0.927$, $L_2 = 0.991$), even with large numbers of juveniles proportionally added to the latters' rings (e.g., 92 juvenile mice; Fig. 3.1). Large residuals were associated with the most extreme PIP values (range: 0.015-0.714), with low range proportions empirically representing relatively few adults to juvenile numbers, and high range ratios representing many adults to juvenile numbers (Fig. 3.4).

Discussion

Heterogeneity was graphically evident over a wide range of population densities in numerous individual murid trapping-web trials (Figs. 3.1-3.3; Table 3.1; Appendices 3-C, 3-D); yet, such behavior had no discernible effect on density estimates. Both white-footed mice and southern red-backed voles exhibited significant age-induced variation in the probability of their capture (i.e., juveniles deferring to adults increasingly as trap-density decreased from inner to outer trapping web rings); behavior previously observed for both murids (e.g., *P. leucopus*: Sheppe 1967, Myton 1974; *C. gapperi*: Watts 1970, Mihok 1979). Nevertheless, despite large amendments of juvenile murids to the outer trapping-web rings of null-heterogeneous models (e.g., Fig. 3.1), paired density estimates remained highly concordant ($r_c = 0.974$) over a wide range of density levels (Fig. 3.3).

These results simultaneously demonstrate two crucial and somewhat diametric aspects of trapping web methodology/analysis (both aspects previously recognized, but seldom, if ever, addressed together). On one hand, as discussed above, significant heterogeneity had no effect on resultant density estimates of murids. This is in accordance with the trapping web and distance sampling/analysis methodology originally outlined by Anderson et al. (1983), and later clarified by Buckland et al. (1993) and

Thomas et al. (2002); the latter stating, “[aside from cluster size]...other sources of heterogeneity contribute little to bias, provided [all animals are detected at web center].” Thus, knowledge of capture-probability models and their assumptions is not required, as with mark-recapture and removal methods—this, advantageous to population estimation. On the other hand, these results also demonstrate the appreciable amount of leverage that the innermost rings of trapping webs exert upon resultant estimates. This is also in accordance with Buckland et al. (1993:348), who state, “...point sampling [is] well named because it is the area near the...point that is critical in nearly all respects”—this, disadvantageous when data from innermost rings is difficult to fit to model estimates.

In this study, trapping web data was often difficult to model-fit due to its vagaries within innermost-rings (i.e., represented by “spikes” or “slumps” in distance histograms); such variation usually caused by as few as one or two murids (Fig. 3.5). Buckland et al. (1993:fig.7.12) state that such data are usually the result of poor survey design or conduct; yet, the options available for such grouped data are limited and prone to subjectivity, and their consideration germane to a discussion regarding heterogeneity. Left-truncating such data is an option (i.e., excise data representing the highly variable inner histogram bar[s]); yet, these data, among all distances sampled from trapping webs should be expected to best-represent “truth” ($f[x]$), and the arbitrary use of left-truncation is seldom recommended (Buckland et al. 1993:15, but see Buckland et al. 1993:284). Remaining options may be: 1) to reduce trap spacing within the inner area of future trapping webs, 2) to further group existent data from inner rings (i.e., essentially increasing trap spacing), or 3) to increase trap spacings throughout future trapping webs (as discussed in Chapter 2). Examination of the empirical data (e.g., Appendix 3-C)

suggests that the reduction of trap spacing within innermost rings may ameliorate the prevalent spiking and slumping of data for moderate-to-high murid population densities if additional traps were placed, for example, 15 m from trapping web centers, joining traps originally spaced at 7.5, 22.5, 37.5, 52.5, 67.5, 82.5, and 97.5 m; this, resulting in a trap-spacing of 7.5 m between the three innermost rings and 15 m between the remaining web rings. Wilson and Anderson (1985a) suggested a similar pattern of trap spacing for small mammals, using a combination of 4.5 m spacing for inner trapping web rings and 6 m or greater spacing for outer rings; however, their intent was to assuage edge-effect in the outermost rings, rather than ameliorate the variability inherent to inner web rings (hereafter referred to as “center-effect”). Reducing trap spacing at web centers, however, is unlikely to eliminate center-effect, given the paucity of murids captured in the innermost rings of most trapping webs, even at moderately high population densities (see Appendices 3-A, 3-C). For example, a single mouse was captured in the innermost ring of a trapping web that contained 110 additional mice, representing a population density of approximately 38 mice/ha. The second option (to further group already grouped data) will generally result in a loss of precision in the estimate, but may often provide a more acceptable fit of model estimate to data and usually results in little change in estimates of density (Buckland et al. 1993:116). The concept supporting the grouping of previously grouped data was applied in this study for the PIPs (i.e., the pooled proportional data from the innermost trapping web rings) used to develop null-heterogeneous models. The third option (to increase trap spacings throughout trapping webs) should ameliorate the displacement of animals toward web centers and potentially reduce spiking; however, this

would reduce a 3-ha trapping web's precision (i.e., by reducing the number of web rings) or necessitate trapping webs larger than 3 ha, in order to use seven or more web rings.

When heterogeneity is recognized in other types of distance sampling data, it is commonly dealt with by stratification or the use of covariates in analysis, thereby potentially improving precision and reducing bias of estimates (Buckland et al. 1993:99). Nevertheless, post-stratification of adult and juvenile mice in the six most heterogeneous trapping web trials in this study (“web1297s2”, “web0297s2”, “web1bf98”, “web3eb98”, “web1se98”, “web2se98”; see Appendix 3-C) suggests constraint in the use of this method for multiple reasons. First, stratified adult data did not lend themselves to distance models as well as stratified juvenile data at most population densities (Fig. 3.6). At lower murid densities, few adult mice were detected within large central trapping web areas, leaving “gaps” within inner histogram data; necessitating the grouping of groups. At higher densities, disproportionate numbers of adult mice were often detected within inner rings and outer rings, these mice (albeit few) mobile despite social fences (Hestbeck 1982); this, calling for either the arbitrary truncation of inner and outer rings prior to analysis, or further investigation regarding the grouping of existent data or an increase in trap spacing throughout trapping webs, as discussed above. Second, there was no significant difference between density estimates of non-stratified and combined post-stratified data (see Table 3.1); thus, little need for post-stratification. Finally, post-stratification artificially reduces within-stratum variance, potentially resulting in the substantial underestimation of variance (S. Buckland, pers. comm.).

In summary, in contrast to the somewhat vague and occasionally contradictory literature on trapping web methodology/analysis (see references above), these results

graphically demonstrate heterogeneity's lack of effect on density estimates, as well as the fact that such heterogeneous data's post-stratification is not necessary (although such stratification may offer behavioral clues leading to more effective use of trapping webs). Further, via this assessment, the problematic aspect of point-sampling sensitivity (i.e., "center-effect") is elucidated, suggesting potential solutions and trade-offs for future trapping web use.

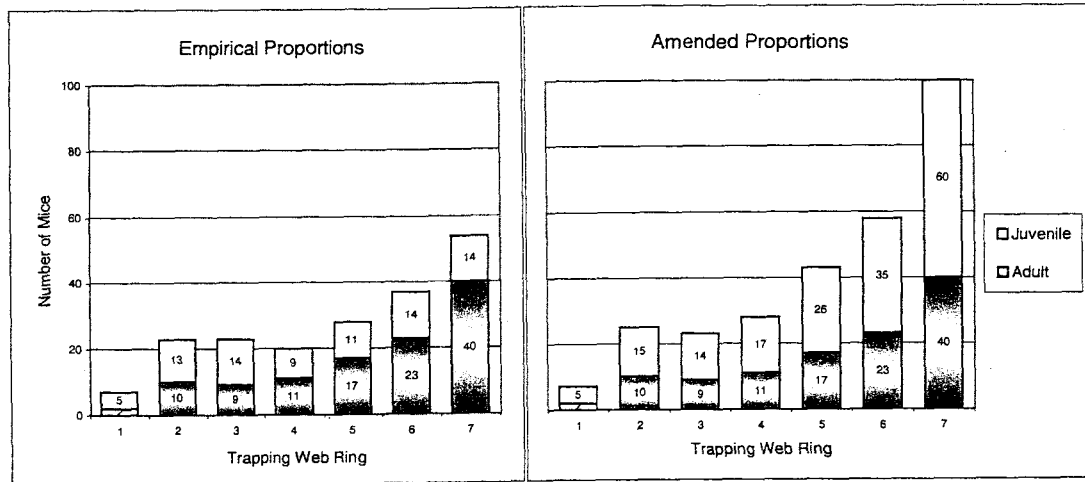


Figure 3.1. Empirical proportions of juvenile and adult white-footed mice (*Peromyscus leucopus*) exhibiting age-induced heterogeneity (trend test: $P < 0.001$) during a trapping web trial in central Massachusetts, October 1998; and their amended proportions after 92 “juveniles” were added to rings 2-7, creating a null-heterogeneous model for this trial.

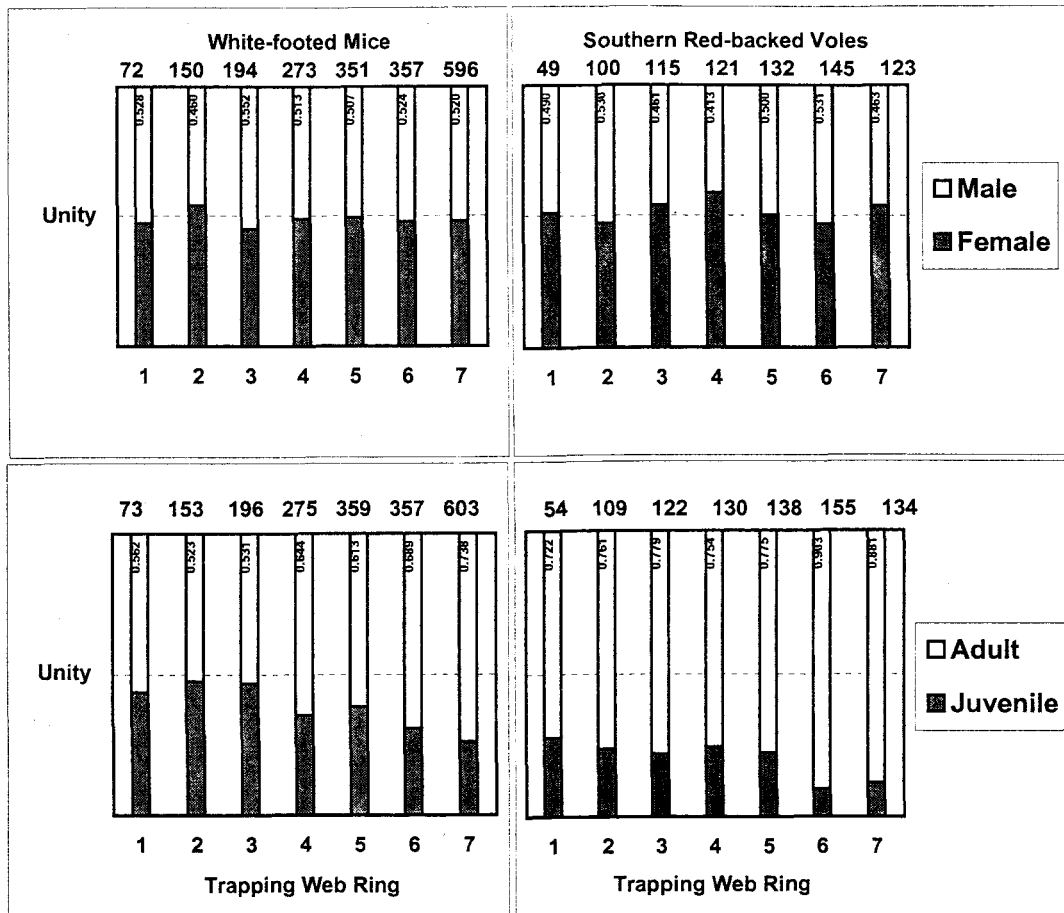


Figure 3.2. Pooled proportions of white-footed mice (*Peromyscus leucopus*) and southern red-backed voles (*Clethrionomys gapperi*) captured during trapping webs trials ($n = 24$, $n = 23$; respectively) performed in central Massachusetts, Aug-Dec 1996-1998. Proportions displayed per species per sequential trapping web ring by sex and age. Ratios within bars, with total number of animals per ring at tops of bars; “unity” = 1:1.

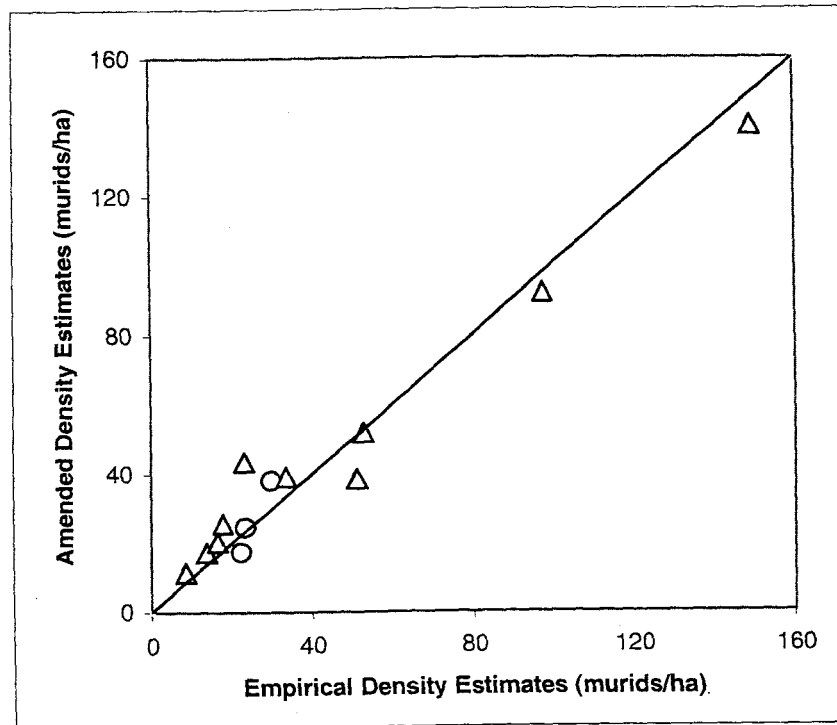


Figure 3.3. Trapping web density estimates determined by empirical trials exhibiting age-induced heterogeneity and their amended null-heterogeneous models ($p_{i1} = n_{i1}/n_i$, equivalent for all rings). Mice ($n = 10$) represented by triangles, voles by circles ($n = 3$). Absolute agreement evinced by data falling on 45° concordance line intersecting origin.

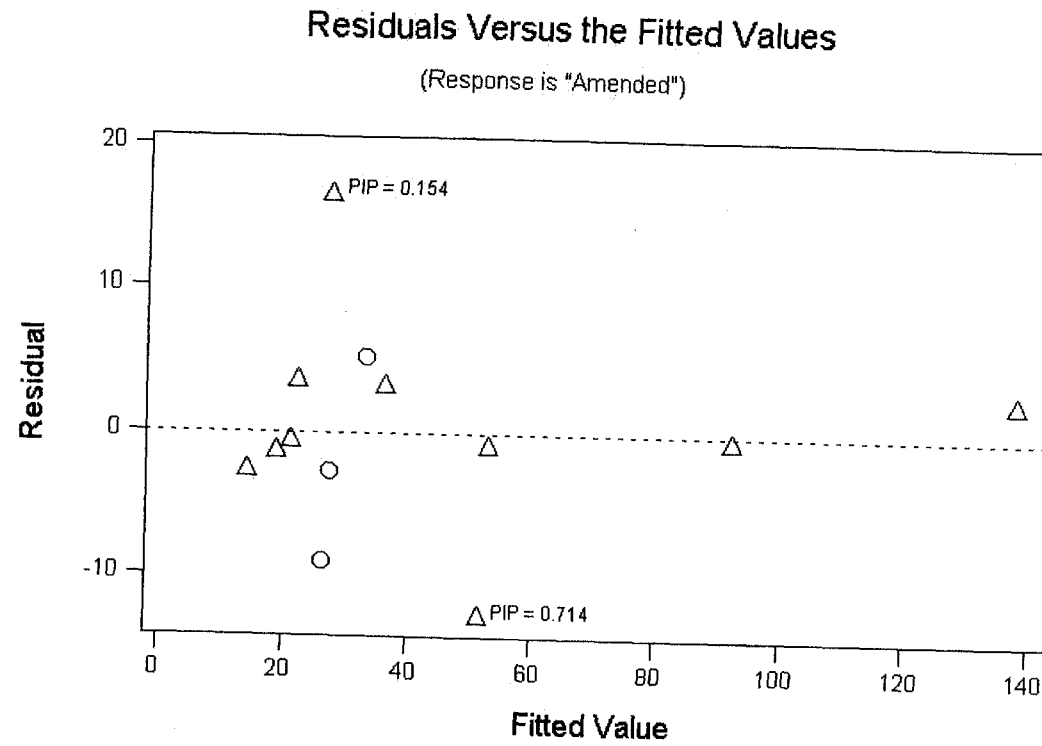


Figure 3.4. Residuals associated with empirical heterogeneous trials and their amended null-heterogeneous models. The largest residuals are associated with extreme PIP values. Mice represented by triangles, voles by circles.

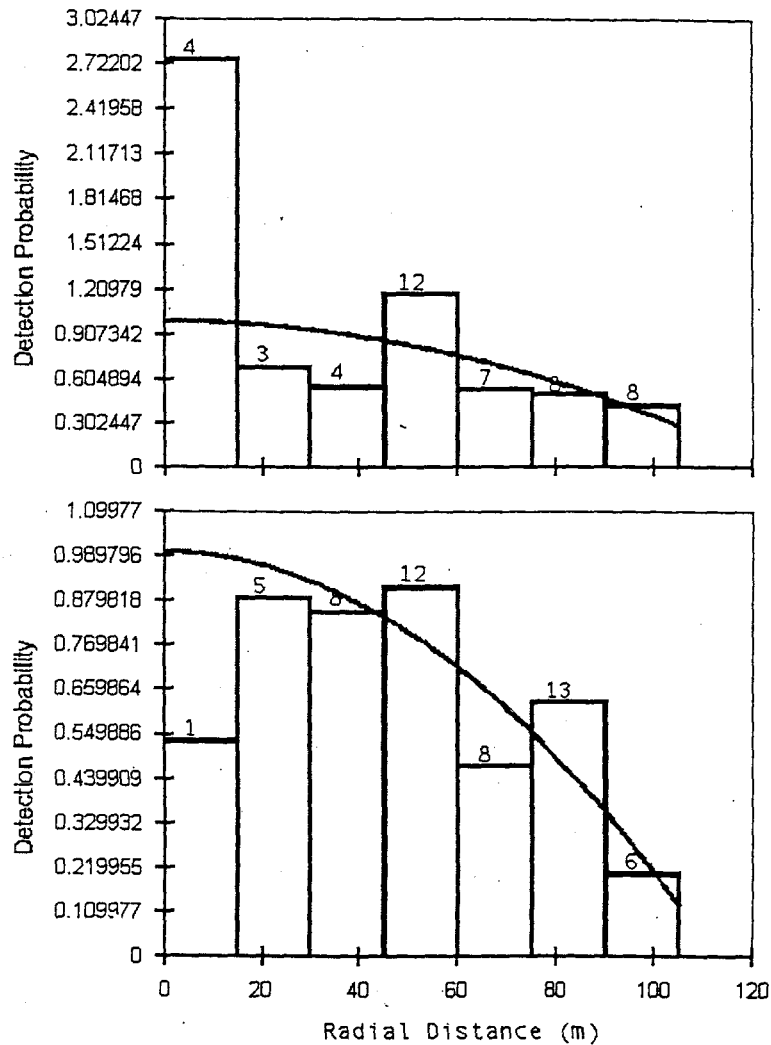


Figure 3.5. Examples of vagaries in empirical trapping web data (i.e., “center-effect”) caused by a few murids within innermost rings and represented as “spikes” or “slumps” in distance histograms. Adjacent 3-ha trapping webs “Web1se97” (bottom) and “Web2se97” (top) were trapped simultaneously during November, 1997, yielding respective *Peromyscus leucopus* density estimates of 23.3 and 20.6 mice/ha.

Figure 3.6. Examples of post-stratified empirical trapping web data from trials exhibiting the most significant age-induced heterogeneity between adult/juvenile white-footed mice (*Peromyscus leucopus*). Truncated adult strata did not model as well as juvenile strata, as evidenced by the detection functions, where curves with some “shoulder” indicate better model fit. Some degree of “edge-effect” was evident in each trial, as evidenced by spikes in outermost web ring (e.g., see “All Mice, entire web”). “Center-effect” was evident, as evidenced by mostly spikes and some slumps, especially when data were post-stratified.

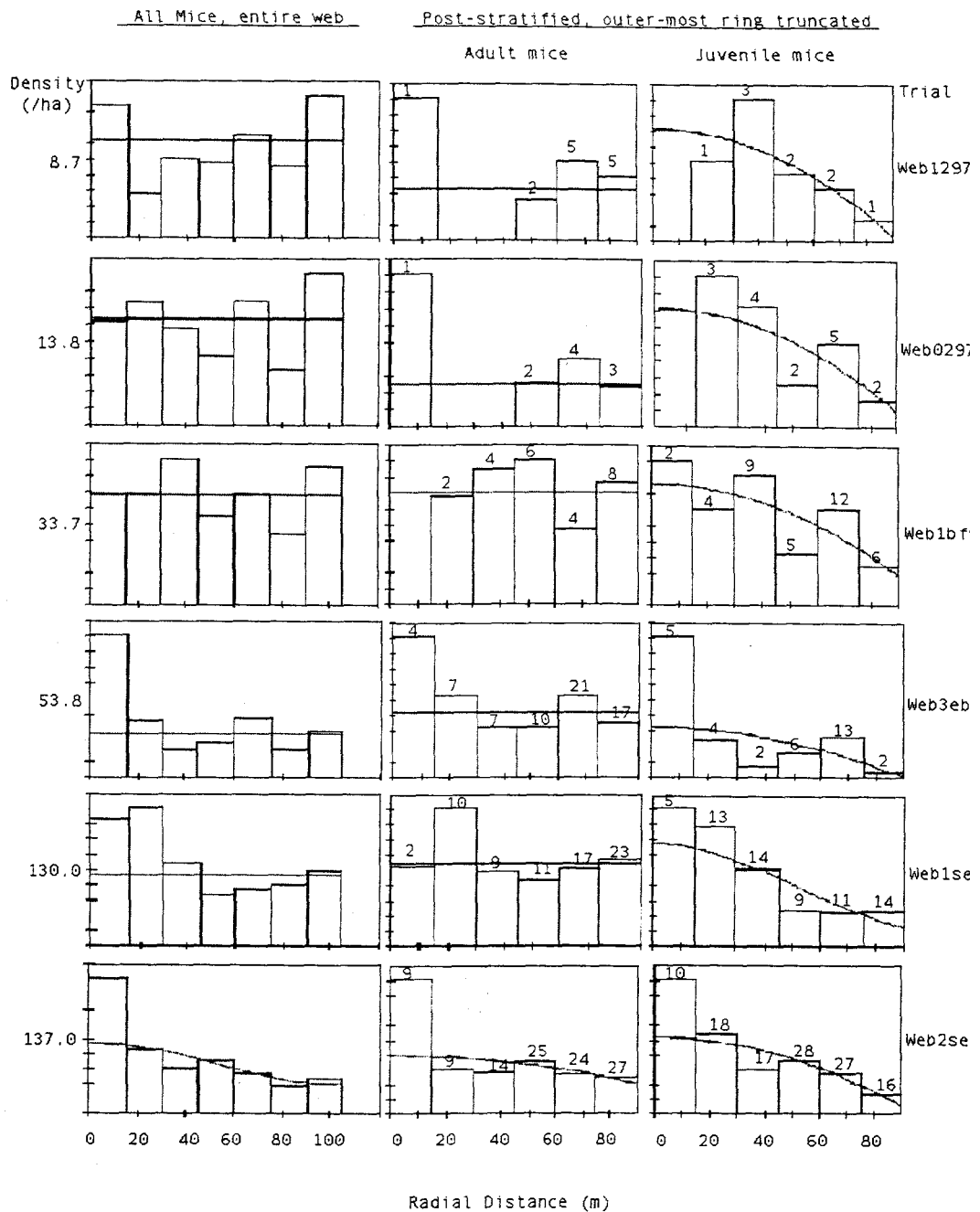


Figure 3.6

most significant age-induced heterogeneity for *Peromyscus leucopus*. Density estimates of non-stratified and combined post-stratified data exhibited no significant differences (two-tailed paired *t*-test: *t* = -0.87, *P* = 0.42). All distance histograms representing these trials were right-truncated prior to analysis due to edge-effect (i.e., only data from the 6 inner-most rings were used for density estimates).

Trial ^a	Non-stratified		Post-stratified		Post-stratified		Post-stratified
	\hat{D}^b (all mice)	CV ^b	\hat{D} (adults)	CV	\hat{D} (juveniles)	CV	\hat{D} (combined)
Web1297s2	8.7	0.213	5.1	0.277	5.6	0.522	10.7
Web0297s2	13.8	0.371	3.9	0.320	11.3	0.330	15.2
Web1bf98	33.7	0.205	9.4	0.204	23.9	0.233	33.3
Web3eb98	53.8	0.190	25.9	0.120	25.0	0.210	50.9
Web1se98	130.0	0.180	69.0	0.206	67.5	0.204	136.5
Web2se98	137.0	0.098	55.5	0.161	81.6	0.122	137.1

^a From Appendix C.

^b Density estimates (\hat{D}) and their coefficients of variation (CV) generated from program DISTANCE.

CHAPTER 4

COMPARISON OF TRAPPING WEB/DISTANCE AND GRID/MARK-RECAPTURE DENSITY ESTIMATES FOR WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*)

Introduction

Population density estimates derived from empirical trapping web data have not previously been evaluated over the range of densities possible for many small mammals, in contrast to the many such inclusive assessments of their population abundance (N) obtained from mark-recapture data (e.g., Lefebvre et al. 1982, Manning et al. 1995, Boulanger and Krebs 1996, Slade and Blair 2000). In their introduction of the trapping web method, Anderson et al. (1983) provided *Peromyscus* spp. capture data from a single trapping session. Jett and Nichols (1987) compared trapping web and nested-grid density estimators using capture data from two trapping sessions of meadow voles (*Microtus pennsylvanicus*), sampled two weeks apart from the same site. Corn and Conroy (1998) provided five trapping sessions of capture data of the small Indian mongoose (*Herpestes javanicus*) from three sites using trapping webs. Parmenter et al. (2003) compared trapping web and mark-recapture grid density estimates using 11 data sets (some pooled across species) representing a total of nine rodent species, most at low population density levels (i.e., ≤ 20.6 rodents/ha). Population level, however, is known to influence the performance of small mammal abundance estimators (see Manning et al. 1995, Boulanger and Krebs 1996); thus, we may also expect abundance per defined area (D) to influence population density estimates derived from trapping-web density estimators.

Acknowledging the effect that population level may have on trapping web density estimates, Wilson and Anderson (1985a) performed Monte Carlo capture simulations of “small mammals” at densities of 25/ha and 100/ha, and Parmenter et al. (1989) provided 12 sessions of darkling beetle (Tenebrionidae: *Eleodes* spp.) capture data using a range of known populations. Unfortunately, generic modeling efforts may not adequately approximate natural populations (e.g., in regard to animal behavior), and, as pointed out by Buckland et al. (1993), darkling beetles do not maintain home ranges (this adverse to a fundamental requirement of the trapping web: that animal movement remain stable [i.e., within home ranges] during sampling sessions). As such, the use of either such models or animals in assessing density estimators involving the trapping web is questionable.

A common approach to estimator evaluation entails the comparison of different estimators of a parameter of interest acquired from the same population (see Jett and Nichols 1987). Estimators are perhaps best evaluated on populations with known parameters (e.g., Mares et al. 1981: eastern chipmunks [*Tamias striatus*] on an island; Manning et al. 1995: gray-tailed voles [*Microtus canicaudus*] in fenced enclosures; Parmenter et al. 2003: various desert rodents in fenced enclosures); yet, we seldom know what these values are for populations of small cryptic mammals, even via “saturation trapping” in enclosures, because many members of a population may prove untrappable. Moreover, individuals from closed populations may exhibit different behavior than their free-ranging counterparts (e.g., Crowcroft and Rowe 1963), and logistic constraints may preclude sufficient replication along the range of potential population densities. Accordingly, in this study, I compare the performance of density estimators associated with the trapping web/distance-sampling design to those used for mark-recapture, both

derived from the same populations of white-footed mice (*Peromyscus leucopus*, hereafter “mice”); these populations representing the entire range of densities previously reported for this species (see Wolff 1989). These results, when considered within the context of previous trapping web assessments of movement by these mice (Chapter 2) and the heterogeneity of their capture probabilities (Chapter 3) will permit inferences about the performance of these methods for a wide range of field situations.

Methods

Capture data for mice were obtained from eight individual, 3-ha trapping webs and eight 0.81-ha mark-recapture grids (each superimposed and centered on a web; these pairings hereafter “web/grids”) located at three forested sites in central Massachusetts, where webs were separated by at least 50 m (see Fig. 1.3). These mature forested sites (> 80 years old) were of the red oak (*Quercus rubra*)-white pine (*Pinus strobus*)-red maple (*Acer rubrum*) forest-cover type (Eyre 1980). These sites were live-trapped between August-December, 1997-98, yielding 28 trials (as 14 web/grid pairs; see Appendix 4-A). Most trapping sessions were five days (paired trials were usually of equal duration), with an average interim of 10 days between paired web/grid trials. These periods were a compromise, allowing captured mice to recover their body weight (thus reducing individual mortality; see Bietz et al. 1977, Kaufman and Kaufman 1994), without great changes occurring in populations. Further, 4-5 day sessions allow assumption of closure for mark-recapture closed-population estimators, while usually providing opportunity for all mice at trapping web centers to be captured, the primary assumption for the trapping web/distance-sampling design. Given that annual mortality for these mice generally leads to a complete population turnover (Lackey et al. 1985), six of eight web/grids were

trapped, as described above, once during both 1997 and 1998 (the other two web/grids established and trapped in 1998); thus preventing pseudoreplication (Hurlbert 1984).

Trapping webs used in this study comprised of 6-16 equidistant lines radiating from their centers (most commonly 12 or 16 “radii”; see Appendix 4-A), along which pairs of Sherman live-traps were placed at 15-m intervals, starting 7.5 m from center out to 97.5 m; this pattern resulted in seven equally-provisioned “rings” totaling 84-224 traps. Mark-recapture grids, following common use (e.g., Elkinton et al. 1996), contained 49 of the same live-traps, singly spaced 15 m equidistant in a 7 x 7 square grid with 90-m sides. Inequalities in trapping areas and the number of traps used between methods were considered inconsequential, given the objective to compare commonly used trap lay-outs, the paradigmatic differences between these methods’ deployment of traps, and the results of prior analyses indicating that the number of web radii (i.e., number of traps) had no significant effect on the summary movement of these mice (see Chap. 2).

Trapping logistics at the two sites that contained three web/grid pairs usually entailed operating two of the grids and one of the webs simultaneously during the first trial, removing these traps for the interim, then trapping the remaining grid and two webs. In such manner, fewer traps were run during first trials when most mice were ear-tagged, and fewer mice required tagging when more traps were run during the second trial. Additionally, by alternately sampling web/grids (see Appendix 4-A) differences incurred by young mice becoming part of trappable populations over interim periods were offset.

Program DISTANCE (Buckland et al. 1993, Laake et al. 1993), ver. 3.5, was used to provide direct estimates of population density (\hat{D}) of mice captured on trapping webs. First-capture data were pooled over each session by trapping web ring, summarized as

$$n_{ij} = n_{ij1} + n_{ij2} + \dots + n_{ijt}$$

where n_{ij} was the number of animals trapped in the j^{th} ring of the i^{th} trapping web.

Letting total sample size be $n = \sum_i \sum_j n_{ij}$, population density was estimated by

$$\hat{D} = \frac{n \cdot \hat{h}(0)}{2\pi k}$$

with $\hat{h}(0)$ obtained through standard point transect methods (Buckland et al. 1993:280).

Data consisted of distances of individual mice from trapping web centers at first capture, with values of “7.5”, “22.5”, “37.5”, “52.5”, “67.5”, “82.5”, or “97.5” m for each mouse.

Intervals were manually assigned using cutpoints of 0, 15, 30, 45, 60, 75, 90, and 105 m, and histograms of grouped data created (by DISTANCE), examined, and—if necessary—

truncated, further grouped, or stratified (see Chapter 3, Discussion) prior to fitting models

(e.g., Fig. 3.6); these alterations often necessary to meet criteria for robust estimation,

such as the criterion that detection functions have “shoulders” (Buckland et al. 1993:74).

Several robust models were used to examine these histograms, including (listed as [key

function] / [series expansion]): half-normal/cosine, half-normal/hermite polynomial,

hazard-rate/cosine, hazard-rate/simple polynomial, uniform/cosine, and uniform/simple

polynomial (Buckland et al. 1993:46). Iterations back and forth between models and

alterations (the latter kept to a minimum, given the inherent limitations of grouped data),

and use of Akaike’s Information Criteria (hereafter “AIC”; generated by DISTANCE)

within groups of models with the same cutpoints/truncation, led to final analyses of

population density; these including DISTANCE-generated coefficients of variation and two-sided 95% confidence intervals based on variances estimated from empirical data. Essentially, the fit of models to data nearest the center point of webs was most critical, and AIC provided an objective, parsimonious selection criteria among potential models.

Program CAPTURE (Otis et al. 1978, White et al. 1982) and the interactive front-end data entry program 2CAPTURE (Rexstad and Burnham 1991), ver. 1, were used to provide population abundance estimates (\hat{N}) of mice captured on mark-recapture grids. These analyses used complete capture histories, based on the Lincoln-Petersen model

$$m_2/n_2 = n_1/N$$

where n_1 is a sample of mice captured, marked, and released; n_2 is a later sample, some of which, m_2 , are marked; and N is the total population (from Lancia et al. 1994:239). Chapman's estimator of population abundance, a modified form with less bias, follows as

$$\hat{N}_c = [(n_1 + 1)(n_2 + 1)/(m_2 + 1)] - 1.$$

CAPTURE was first used to screen mark-recapture data for behavioral responses or high heterogeneity in individual capture probabilities (Menkens and Anderson 1988), following examples of annotated CAPTURE output provided by White et al. (1982:132). If such sources of variation were present, the model selection procedure provided by CAPTURE was used (taking into consideration the biological results from Chapter 3, where age-induced variation in the probability of capture of mice was evident over the

entire range of population densities) to select the appropriate closed-population estimator, with the exception of null model “ M_0 ” (the “equal catchability model”), which can be highly biased if there is unequal capture probability; thus, non-applicable to real data (White et al. 1982:165). Further exception to the use of the model-selection procedure of CAPTURE was made when the number of individual mice captured was less than 20 or their average probability of capture (“ \hat{p} ”; generated by CAPTURE) was less than 0.3 (White et al. 1982:165); in which case, Chapman’s estimator (see above) was used to estimate population size (Menkens and Anderson 1988, Manning et al 1995).

Estimates of density (\hat{D}) were manually generated using Dice’s (1938) concept of a boundary strip (with area “ W ”) added around the outside of the mark-recapture grid (with area “ A ”), where the width of W is half of the mean maximum distance moved (hereafter “MMDM”; generated by CAPTURE) by mice captured more than once; thus

$$\hat{D} = \frac{\hat{N}}{(A + W)},$$

computed for this study (as mice per hectare) as

$$\hat{D} = \frac{\hat{N}}{\left(\frac{[90 + MMDM (15)]^2}{10,000} \right)}.$$

Confidence intervals for density estimates were similarly generated from CAPTURE-generated, two-sided 95% confidence intervals for \hat{N} , as were coefficients of variation for density estimates from CAPTURE-generated standard errors for \hat{N} , computed as

$$CV(\hat{D}) = \left(\frac{S.E.(\hat{N})}{\hat{D}} \right).$$

Dice (1941) emphasized his method's subjective limitations; yet, many researchers continue to present their results based on this measure (e.g., Corn and Conroy 1998). Also, Tanaka (1980), having reviewed methods of determining effective area, including nested grids and assessment lines, concluded that Dice's method remained superior to all existing methods (Wilson and Anderson 1985b, but see Parmenter et al. 2003).

Ultimately, density estimates derived from paired web/grids were compared and evaluated using both paired-sample *t*-tests and concordance correlation (Lin 1989, Zar 1996:401, see Chapter 3). Concordance correlation provides a superior index of the agreement between two estimates from the same population by measuring variation from a 45° line through the origin (the "concordance line") and is robust with samples as small as $n = 10$ (Lin 1989). Biological data describing movement by mice (Chapter 2) and their age-induced capture heterogeneity (Chapter 3) were employed to explain departures from the concordance line; these portrayed using graphical comparisons of the number of individual mice captured on trapping webs and on paired mark-recapture grids over a gradient of population density, and quantified using linear trend tests and null hypotheses of "no trend" (Zar 1996:562). All tests used a significance level of $P < 0.05$.

Results

Overall agreement between density estimates generated by the trapping web/DISTANCE method and those derived from the mark-recapture/CAPTURE-Dice method for the same populations of mice was “mediocre” (Lin 1989; concordance correlation: $r_c = 0.713$; 95% CI: $L_1 = 0.691$, $L_2 = 0.734$; see Fig. 4.1), and a t -test of all paired data indicated no significant difference (two-tailed: $t = -0.222$, $df = 13$, $P \approx 0.83$). Coefficients of variation ($CV[\hat{D}]$) indicated greater relative precision for mark-recapture estimates than for their paired trapping web estimates in 11 of 14 cases (see Table 4.1); 79% of the CVs for mark-recapture estimates reflected good precision (i.e., $\leq 20\%$; White et al. 1982:50), whereas only 29% of the CVs for trapping web estimates did. Both methods produced a few CVs ca. 50% or greater at low- to mid-level densities (these capable of indicating only order-of-magnitude changes in population density). Similarly, confidence intervals for mark-recapture estimates were generally much smaller than those for trapping webs (Table 4.1); the former occasionally entirely subsumed by trapping web CIs. Thus, individual comparisons of web/grid estimates using their 95% confidence intervals revealed significant differences in only three of 14 (21%) cases; in all of which, CAPTURE estimates were greater than those generated by DISTANCE.

Examination of the plotted paired data, however, revealed systematic differences between the two estimation methods for populations by site and year (Fig. 4.1). At low- to mid-level densities (ca. < 50 mice/ha), mark-recapture/CAPTURE estimates were greater, but at highest densities, trapping web/DISTANCE estimates were greater; this quantified by t -tests of data below the concordance line (one-tailed: $t = 4.701$, $df = 10$, $P < 0.001$) and above the concordance line (one-tailed: $t = -2.456$, $df = 2$, $P \approx 0.06$). Also,

examination of site/year data using Pearson's correlation coefficient as a measure of linear precision (Lin 1989) (excluding "bf site 1998" data, given the meaninglessness of this measure for two points) revealed differences in precision between site/year data (*eb* '97, $r_p = 0.381$; *se* '97, $r_p = 0.684$; *eb* '98, $r_p = 0.992$; *se* '98, $r_p = 0.988$; see Fig. 4.1). As such, biological data pertinent to populations of mice by site/year were considered.

The proportion of individual mice captured on trapping webs compared to those captured on paired mark-recapture grids increased with population density (trend test: $\chi^2 = 43.3$, $df = 1$, $P < 0.001$). This result was expected, given the greater size of trapping webs and numbers of traps employed; however, examination of paired histogram data (Fig. 4.2) revealed two crucial trends. First, ratios of mice captured from lower-density populations were approximately equal, indicating these grids captured more mice from beyond their boundaries than did webs. The pervasiveness of this trend became evident when numbers of adult mice (generally making greater movements than non-adults) captured on grids (0.81 ha) were compared only to those captured on the inner four rings of webs (0.87 ha) (Fig. 4.3); in which, as also expected, the proportion of adult mice captured on grids to those captured on inner webs decreased with population density (trend test: $\chi^2 = 29.399$, $df = 1$, $P < 0.001$), yet, generally remained greater through low- and mid-level densities. Second, numbers of mice captured on mark-recapture grids stabilized at higher densities, suggesting that single traps on these grids were becoming saturated with dominant adults. This trend was perhaps best illustrated by the comparison of adult and non-adult mice captured on mark-recapture grids (Fig. 4.4), in which the proportion of adults to non-adults increased as more adults were captured (trend test: $\chi^2 = 27.011$, $df = 1$, $P < 0.001$).

Discussion

These results suggest crucial systematic differences in the performance of mark-recapture/CAPTURE-Dice and trapping web/DISTANCE density estimation methods relative to the population levels of white-footed mice and similar small mammals. Mark-recapture estimates were consistently greater at low- to mid-level densities, whereas trapping web estimates were greater at the highest densities sampled (see Fig. 4.1)—these site/year-grouped differences suggesting offsetting influences, likely caused by analytical artifact, as well as population level-induced biological characteristics. Similarly, Jett and Nichols (1987), comparing trapping web and nested grid (i.e., mark-recapture) density estimates of a single high-density population of meadow voles (see Reich 1981), found their trapping web estimate greater than their nested grid estimate (trapping web: $\hat{D} = 112.0$, SE = 14.56, CV = 0.13; nested grid: $\hat{D} = 99.0$, SE = 15.77, CV = 0.16); however, their two estimates did not differ significantly (or provide the authors sufficient reason to pursue artifactual or biological explanations for potential differences). Also similarly, Parmenter et al. (2003:table 10: mean per test data set; i.e., “population”), comparing trapping web and mark-recapture grid estimates of “known” low-density populations of various desert rodents with the assistance of expert analysts, found their grid estimates generally greater than their trapping web estimates; this suggesting artifactual constraint in the generation of mark-recapture estimates of effective trapping area.

Examination of biological data describing the movement and age-induced capture heterogeneity of white-footed mice revealed two trends that provide explanations for the systematic offsetting differences found between methods’ density estimates in this study. First, at low- to mid-level densities, mark-recapture grids captured proportionally more

mice from beyond their bounds than did trapping webs (most evident at lowest densities; see Fig. 4.2), ultimately reversing at the highest densities sampled [see age-stratified data, Fig. 4.3]) suggesting greater movement by mice than indicated by CAPTURE-generated MMDMs; this leading to positively-biased CAPTURE estimates at these density levels.

Second, at high population densities, traps on mark-recapture grids became saturated with dominant adult mice to the exclusion of non-adult mice; this, in addition to a general decrease in movement with increased population density (and a potential decline in differences between actual and computed effective trapping areas), leading to negatively-biased CAPTURE estimates at high density levels. (Boulanger and Krebs [1996] considered the heterogeneity/jackknife estimator [M_h]; the model used in this study's analyses of all high density populations; see Table 4.1] relatively robust to bias caused by trap saturation; yet, it is difficult to equate their simulations of 20-400 snowshoe hare [*Lepus americanus*] on 8 x 10 grids with 71-m trap spacing to this study's results, given [as noted] simulations must incorporate the actual biology of the animals being studied).

Such differences between method estimates at high population densities may also have been increased by capture frequency spikes in the innermost rings of trapping webs, given all "se 1998" sites exhibited such spikes (see Table 4.1); these likely exacerbated by high numbers of non-adult mice captured at two of three web/grid centers (Fig. 4.5). Frequency spikes in trapping webs' innermost rings, however, also occurred at lower population densities (see Table 4.1); thus, underestimation of effective trapping area for mark-recapture density estimates due to inadequate MMDMs appeared to be the dominant offsetting influence at low- to mid-level density levels for these comparisons, similar to that observed in most cases by Parmenter et al. (2003).

The trend at low- to mid-level densities, in which mark-recapture grids captured proportionally more mice from beyond their bounds than did trapping webs, may be somewhat explained mechanistically. Mark-recapture grids provided a relatively “solid” matrix of traps, whereas trapping webs provided a gradient of trap densities with traps “feathered” in outermost areas (see Fig. 1.3), effectually diluting “edge-effect” on webs. Nevertheless, trapping webs remain largely affected by “edge-effect” (see Chapter 2), and many other studies have observed murid movement to be dependent on trap spacing (Kikkawa 1964, Tew et al. 1994) and grid size (Faust et al. 1971, Bowman et al. 2001a). As such, it remains likely that MMDMs generated from the mark-recapture grids used in this study were insufficient to accurately represent the actual effective trapping areas.

Further support for the inadequacy of MMDMs may be had by comparison of this study’s mark-recapture-generated MMDMs and trapping web-derived MMDMs (the latter computed after having screened obvious trap-mediated distances of 0, 15, 30, and 45 m; see Chapter 2:figs. 2.7-2.11), in which trapping web MMDMs were generally greater ($\bar{x} = 30.7$ m, SE = 1.83) than mark-recapture MMDMs ($\bar{x} = 17.6$ m, SE = 1.58) by a factor of 1.75 (see Table 4.1). Similarly, Wilson and Anderson (1985b), simulating populations of “small mammals” at densities of 25/ha and 100/ha under different spatial patterns using 7-m trap spacing, CAPTURE-generated MMDMs, and Dice’s (1938) boundary strip method, consistently generated positively-biased density estimates, due likely to insufficient—though relatively large—MMDMs (i.e., $\bar{x} = 33.2$ m, SE = 0.13), very similar to those derived from trapping webs in this study (see above). Their results differed importantly, however, in that their high-density estimates exhibited more positive bias than their low-density estimates; this likely due to their models’ failure to

approximate the age-induced heterogeneity exhibited by real mice in this study (i.e., where adults excluding non-adults from traps at high densities likely reduced estimates). Clearly, the usefulness of population density estimators depend on how closely their underlying model assumptions approximate actual conditions (Jett and Nichols 1987).

Just as clearly, further inference regarding this study's results is not possible without knowledge of the true populations of mice within given areas. Identifying those factors responsible for differences between paired estimates is difficult, given potential interactions between contributing factors (e.g., at the highest population densities). Further, confidence intervals and CVs for density estimates generated by DISTANCE were relatively large and imprecise compared to those derived from CAPTURE (see Table 4.1); thus, dispersive to the elucidation of actual differences. Nevertheless, examination of the paired intersecting confidence intervals on the original concordance plot (Fig. 4.6) supports the premise of offsetting systematic trends addressed above. Although wide, DISTANCE-generated confidence intervals for most of the highest densities did not cross the concordance line, nor would have many CAPTURE-derived confidence intervals, even if doubled; and of the three significantly different individual web/grid pair estimates, CAPTURE-derived estimates were greater in all three cases.

In summary, these results suggest systematic differences in the performance of mark-recapture/CAPTURE-Dice and trapping web/DISTANCE density estimation methods relative to population levels. CAPTURE estimates were positively-biased at this study's low- to mid-level densities and likely negatively-biased at high-level densities; this supported by biological data delineating movement by white-footed mice and age-induced heterogeneity in their capture. DISTANCE estimates may have been positively-

biased at the highest densities observed, given that historical mark-recapture population density estimates for these mice in central Massachusetts have ranged from 1–126/ha, with a mean density of 27.8/ha, SD = 30.6 (9 years data; W. Healy, USDA Forest Service, personal comm.). Alternatively, it is possible these historical estimates were gravely negatively biased. Population levels of 115 white-footed mice per hectare, and 109 and 163 deer mice (*Peromyscus maniculatus*) per hectare have also been reported (see Wolff 1989:281); however, if non-adult (yet trappable) mice were largely excluded in these estimates, actual densities of such mice may have existed as high as 200–400/ha, similar to the highest population density estimate generated by DISTANCE in this study. Such high densities, however ephemeral, would likely require those studies modeling the ecological effects of mice and similar small mammals to adopt a panoply of new metrics.

The trapping web/distance sampling method is not without problems of its own (see Chapters 2 and 3); however, as shown above, webs provide a gradient of metrics against which mark-recapture/CAPTURE and other estimation methods may be assessed. Other similar work, such as that performed by Parmenter et al. (2003), using paired trapping webs and mark-recapture grids on small mammal populations of “known” size within an enclosed area, provide useful information (as would computer simulations that more closely approximate target animal behavior). However, even “saturation trapping” within restricted areas, as practiced by Parmenter et al., may fail to capture all existing animals (e.g., Mares et al. 1981: where ca. 10% of the eastern chipmunks released on an island were not re-captured). As such, empirical comparisons such as those performed by Parmenter et al. (2003) may not be definitive, especially at low population density levels.

Future similar work should consider the use of neutered, possibly electronically monitored small mammals that are released within large predator-free enclosures.

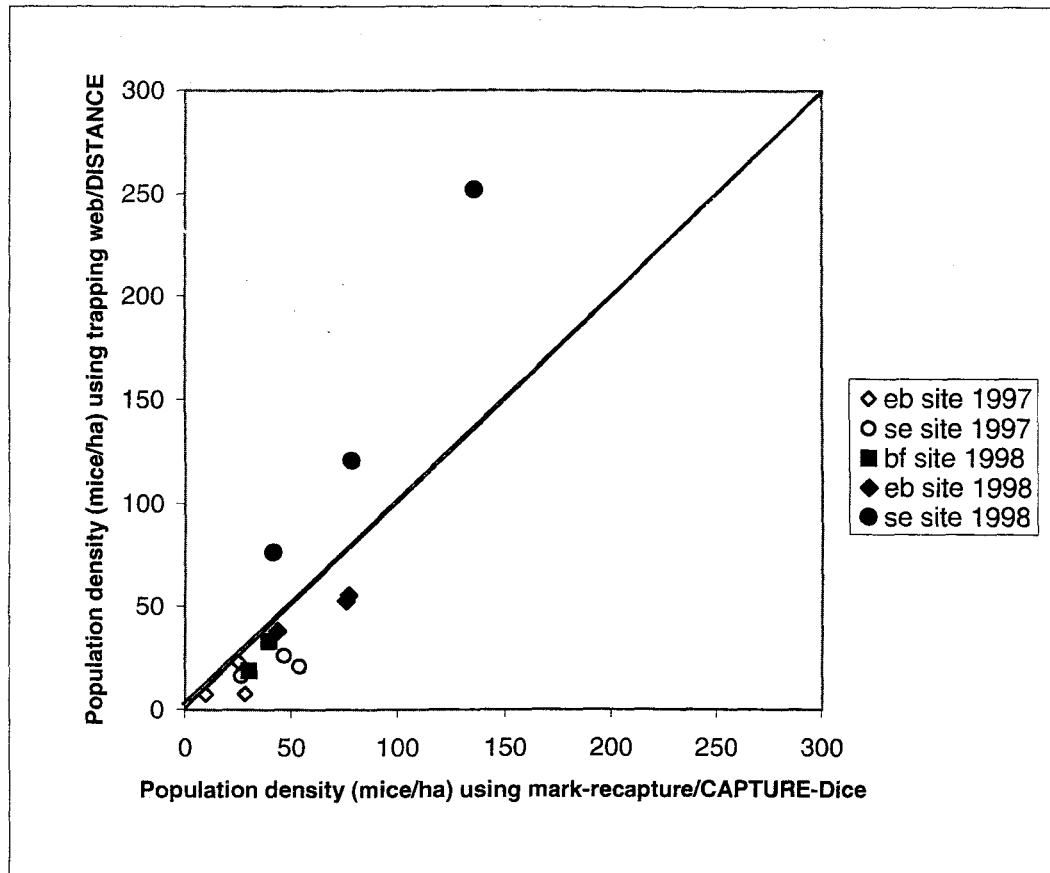


Figure 4.1. Concordance-correlation plot indicating mediocre agreement ($r_c = 0.713$) between paired trapping web/DISTANCE and mark-recapture/CAPTURE-Dice density estimates for populations of white-footed mice (*Peromyscus leucopus*) live-trapped on eight superimposed web/grids at three forested sites in central Massachusetts, 1997-98. Absolute agreement evinced by data falling on 45° concordance line intersecting origin.

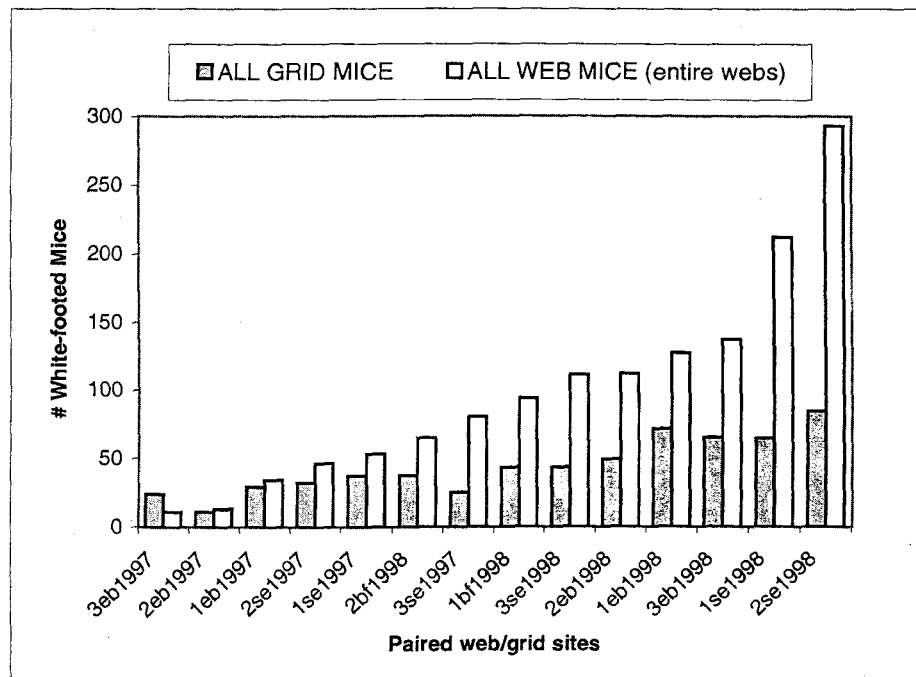


Figure 4.2. Total numbers of individual mice captured on entire trapping webs and paired mark-recapture grids over a gradient of population density, sorted by web mice.

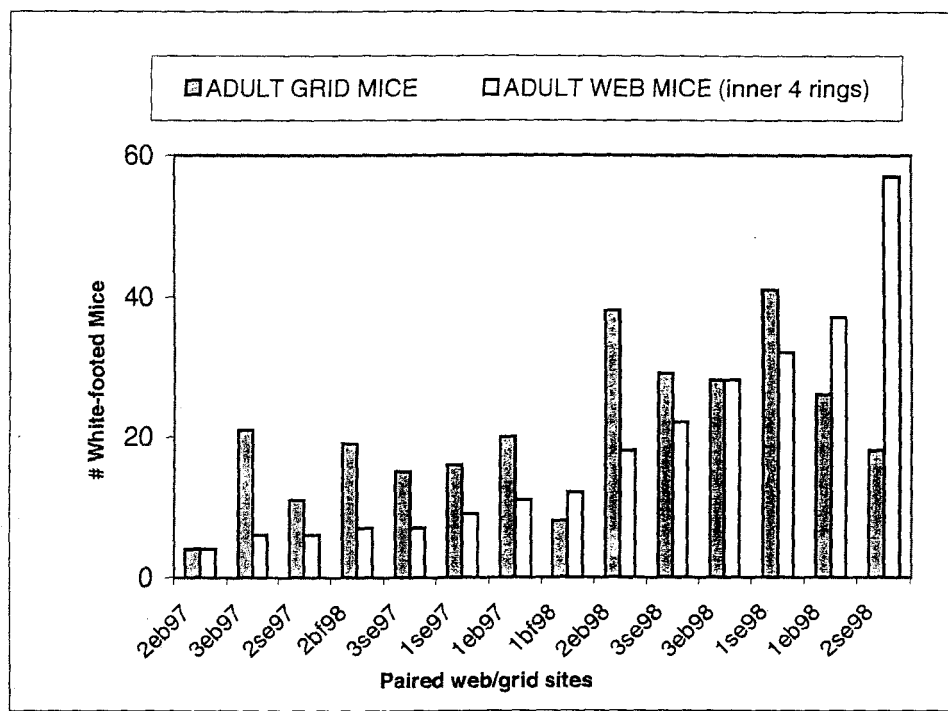


Figure 4.3. Individual adult mice captured on inner four rings of trapping webs and paired mark-recapture grids over a gradient of population density, sorted by web mice.

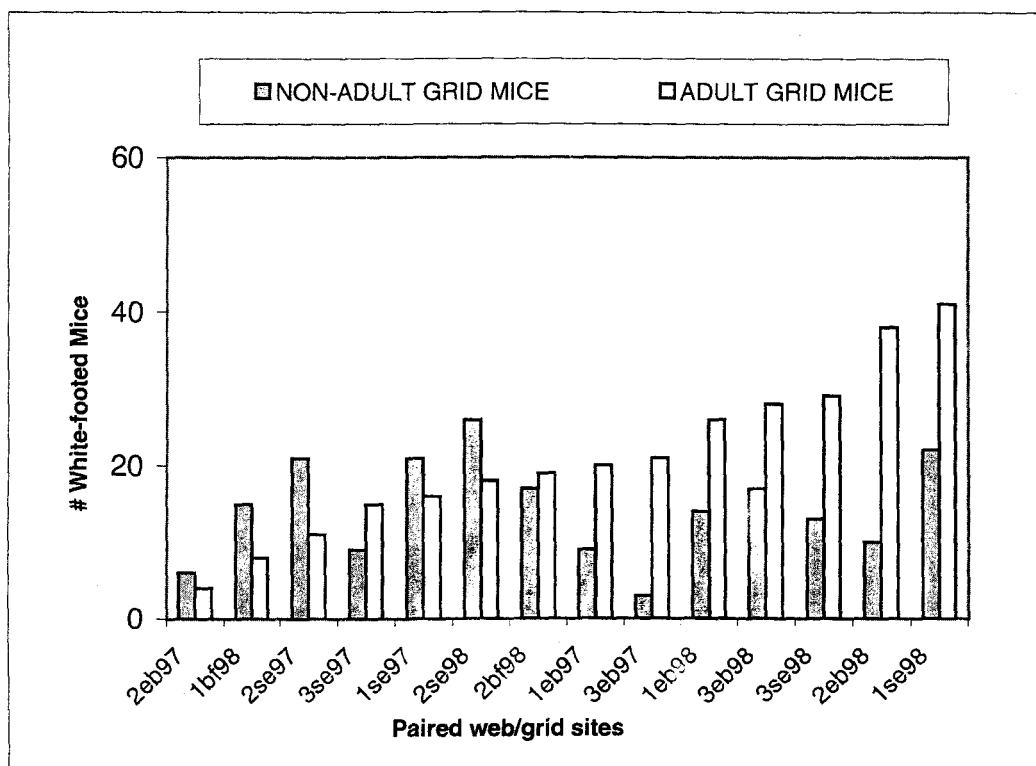


Figure 4.4. Individual non-adult and adult mice captured on mark-recapture grids over a gradient of population density, sorted by adult mice.

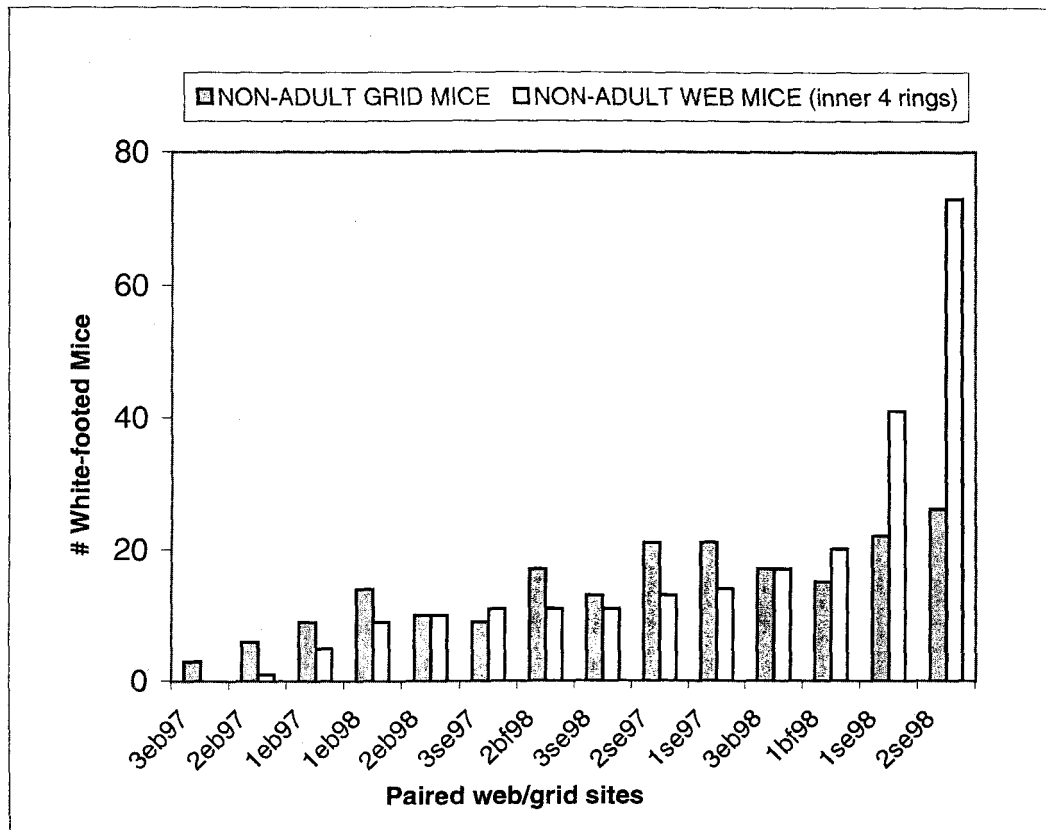


Figure 4.5. Individual non-adult mice captured on inner four rings of trapping webs and paired mark-recapture grids over a gradient of population density, sorted by web mice.

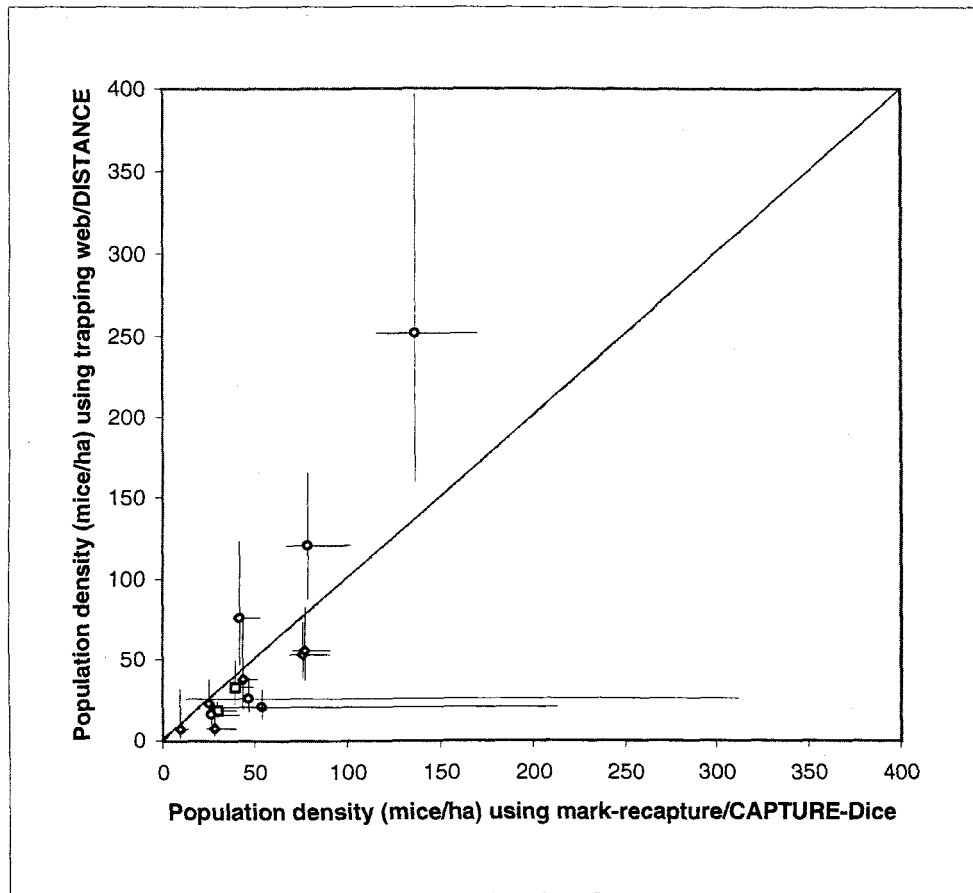


Figure 4.6. Concordance plot with paired intersecting 95% confidence intervals.

TABLE 1. ESTIMATES OF DENSITY, CAPTURE PROBABILITY, AND RELATED STATISTICS. Trials (yr = 1997) listed as site-year, by grid then web.

Paired trials (site name/yr)	\hat{D} (mice/ha)	CV (%)	95% C.I. (or P.L.I. ¹)	Model ²	MMDM ¹¹ (m)	Number of adults	Number of non-adults	Total ¹³ mice
Grid1eb97	25.28	3.21	25.3 – 27.9 ¹	Time+Behavior/Burnham	17.1	20	9	29
Web1eb97	23.01	24.57	14.1 – 37.7	Uniform/Cosine	16.4	20	13	33
Grid2eb97	9.72	30.86	5.6 – 13.8	Lincoln-Peterson/Chapman ^{3, 4}	30.0	4	6	10
Web2eb97	7.24	67.00	1.6 – 32.1	Half-normal/Cosine ^{8, 10}	— ¹²	7	6	13
Grid3eb97	28.21	15.45	23.8 – 39.7	Heterogeneity/Jackknife ³	16.5	21	3	24
Web3eb97	7.51	42.93	3.0 – 18.8	Uniform/Cosine	— ¹²	9	2	11
Grid1se97	69.93 ⁵	96.37 ⁵	36.2 ⁴ – 334.8 ⁵	Behavior/Zippin ⁵	20.3	16	21	37
Web1se97	25.90	18.62	17.9 – 37.5	Uniform/Polynomial	26.1	20	27	47
Grid2se97	54.16 ⁶	73.81 ⁶	31.8 – 213.2 ⁶	Behavior/Zippin ⁶	17.9	11	21	32
Web2se97	20.58	21.46	13.4 – 31.6	Uniform/Polynomial ¹⁰	33.1	18	23	41
Grid3se97	26.44	14.22	24.6 – 41.6	Time+Hetero./Chao (M_{th})	12.9	15	9	24

Grid1bf98	39.55	7.22	37.8 – 49.0	Heterogeneity/Chao (M_h)	17.9	8	15	25
Web1bf98	32.97	20.69	21.9 – 49.7	Uniform/Polynomial ⁹	35.8	45	49	94
Grid2bf98	29.99	13.33	27.8 – 40.0	Heterogeneity/Jackknife	28.4	19	17	36
Web2bf98	18.77	12.40	14.7 – 24.0	Uniform/Cosine	38.8	29	28	57
Grid1eb98	77.32	7.27	71.0 – 91.0	Heterogeneity/Jackknife	14.9	26	14	40
Web1eb98	55.54	20.12	37.4 – 82.5	Uniform/Cosine ⁹	30.3	103	22	125
Grid2eb98	43.52	4.93	42.9 – 51.4	Behavior+Hetero./Removal	18.0	38	10	48
Web2eb98	37.98	34.07	19.3 – 74.6	Half-normal/Cosine ⁷	33.2	70	34	104
Grid3eb98	76.16	7.38	69.4 – 90.6	Heterogeneity/Jackknife	11.9	28	17	45
Web3eb98	52.67	16.33	38.2 – 72.7	Uniform/Polynomial ^{9, 10}	30.7	100	36	136
Grid1se98	78.91	11.43	68.0 – 101.6	Heterogeneity/Jackknife	15.0	41	22	63
Web1se98	120.58	16.10	87.8 – 165.5	Uniform/Cosine ^{8, 10}	28.3	112	80	192
Grid2se98	136.12	9.38	116.1 – 169.9	Heterogeneity/Jackknife	7.4	18	26	44
Web2se98	251.68	23.42	159.6 – 396.8	Half-normal/Cosine ^{9, 10}	24.3	147	142	289
Grid3se98	41.89	9.52	38.5 – 53.0	Heterogeneity/Jackknife	18.2	29	13	42
Web3se98	76.04	24.32	46.8 – 123.6	Uniform/Cosine ^{7, 10}	38.6	75	28	103

¹ Profile Likelihood Interval used when 95% C.I. (based on symmetrical $\hat{D} \pm 1.96[\text{SE}]$) nil; interval based on the asymptotic χ^2 distribution of the generalized likelihood ratio test (see Rexstad and Burnham 1991:20).

² CAPTURE closed-pop models listed as [model]/[estimator], DISTANCE models listed as [key function]/[series expansion].

³ Null model (M_0) selected by CAPTURE.

⁴ Followed Pollock et al. (1990:11) in estimation of N , Var/S.E., and C.I., given both the low capture of mice ($n < 20$) and capture probability ($\hat{p} < 0.3$). MMDM estimated as 2.0 (30m), based on maximum empirical MMDM.

⁵ Next best model 'time and behavior' (Burnham M_{tb}): $\hat{D} = 41.14$ mice/ha, CV(%) = 49.57, 95% C.I. (32.1 – 125.1).

⁶ Next best model 'time and behavior' (Burnham M_{tb}): $\hat{D} = 34.39$ mice/ha, CV(%) = 32.22, 95% C.I. (28.4 – 80.0).

⁷ Three outer rings of trapping web truncated.

⁸ Two outer rings of trapping web truncated.

⁹ Outer ring of trapping web truncated.

¹⁰ Innermost rings of trapping web "spiked" (high number of captured mice relative to immediately adjacent rings).

¹¹ MMDMs computed for trapping webs after having screened obvious trap-mediated distances of 0, 15, 30, and 45 m (see Chapter 2:figs. 2.7-2.11), CAPTURE-generated for mark-recapture grids.

¹² Computation of MMDMs not possible, those mice captured were not observed to move between trap stations.

¹³ Total numbers of mice identified to age-class (Appendix A lists total numbers of mice captured).

APPENDIX A

FOUR ASSUMPTIONS NECESSARY FOR THE TRAPPING WEB

Four assumptions necessary for consideration of the trapping web distance-sampling design, in the order of their importance (see Anderson et al. 1983).

1. Small mammals at the center of the web are captured with probability = 1 by the end of t occasions (the number of times traps are checked during a session).
2. Animal movement is “stable” with respect to the trapping web; this implying no directional movement by animals, especially toward web centers.
3. Distances from the center of the web to each trap are measured accurately.
4. Animal captures are independent events.

APPENDIX B

PROGRAM USED TO CALCULATE DISTANCES ON TRAPPING WEBS

Program used to calculate all possible distances between a set of capture points for individual, ear-tagged white-footed mice (*Peromyscus leucopus*) captured more than once on trapping webs. Written by Robert T. Brooks, Amherst, Massachusetts.

```
REM CALCDIST.BAS: a program to calculate all possible distances between a set of
points.
REM dimension point arrays to the number of trap nights plus 1
DIM x(10), y(10)
REM initialize end of file check
lastrec = 0
REM open data and output files
REM RENAME FILE NAMES AS APPROPRIATE
OPEN "[filename].txt" FOR INPUT AS 1
OPEN "[filename]" FOR OUTPUT AS 2
REM read first record and set tag number and location
INPUT #1, tag, x(1), y(1)
REM initialize count of number of captures
numcaps = 1
REM LPRINT tag, x(1), y(1), numcaps
REM read balance of captures for a tag number
10 FOR ncap = 2 TO 10
REM read all capture locations for a tag number
INPUT #1, nexttag, x(ncap), y(ncap)
REM LPRINT ncap, tag, nexttag, x(ncap), y(ncap), numcaps
REM exit if at end of file
IF EOF(1) THEN GOTO 29
REM check if new tag number
REM if new number, exit read loop
IF (tag <> nexttag) THEN GOTO 20
REM increase count of number of captures
numcaps = numcaps + 1
NEXT ncap
REM if only one capture, reinitialize variables
REM if two or more captures, go to distance calculation
20 IF (numcaps > 1) THEN GOTO 30
REM write tag number for single captures
WRITE #2, tag
REM reinitialize variables to new tag number
numcaps = 1
tag = nexttag
x(1) = x(2)
```

```

y(1) = y(2)
GOTO 10
REM set end of file check to indicate last record
29 lastrec = 1
REM account for last input record
numcaps = numcaps + 1
REM calculate distance for each possible combination of captures
30 FOR i = 1 TO numcaps
  FOR j = 2 TO numcaps
    REM skip duplicate combinations of captures
    IF i >= j THEN GOTO 39
    REM LPRINT i, j
    REM calculate difference in x- and y-coordinates
    xdist = (x(i) - x(j)) ^ 2
    ydist = (y(i) - y(j)) ^ 2
    REM calculate distance between capture locations
    dist = SQR(xdist + ydist)
    REM LPRINT xdist, ydist, dist
    REM write tag number, capture numbers, and distance
    WRITE #2, tag, i, j, dist
  39 NEXT j
NEXT i
REM exit program at end of file
IF lastrec = 1 THEN GOTO 40
REM reinitialize variables
tag = nextag
x(1) = x(numcaps + 1)
y(1) = y(numcaps + 1)
numcaps = 1
GOTO 10
REM close files and exit
40 CLOSE 1
CLOSE 2
END

```

FREQUENCY OF NET RADIAL MOVEMENT ON TRAPPING WEBS

Frequency of net radial movement values (NET_MOVE) generated by white-footed mice per concentric trapping web ring (15-m apart) during 24 live-trapping trials performed throughout central Massachusetts between August-December, 1996-98. Negative values represent net radial movement toward outermost rings; positive values represent similar movement toward innermost rings. Movements' originating points were the ring of first capture, the ring of final capture determined net radial movement. Shaded areas highlight unobservable value categories.

NET_MOVE	Ring 1	Ring 2	Ring 3	Ring 4	Ring 5	Ring 6	Ring 7	Total
-4	0	1	2					3
-3	4	1	0	1				6
-2	5	4	8	11	16			44
-1	11	18	29	47	49	53		207
0	45	75	91	108	123	132	274	848
1		24	34	44	67	65	107	341
2			6	6	19	13	17	61
3				1	4	6	8	19
4					0	3	1	4
5						1	2	3
Total	65	123	170	218	278	273	409	1,536

TRAPPING WEB FREQUENCIES OF INDIVIDUAL WHITE-FOOTED MICE BY SEX

Trapping web capture frequencies of individual white-footed mice per sex per trapping web ring, sorted by total captured; all ages included. Mice were live-trapped at 12 individual trapping webs at seven sites from 1996-98, in central Massachusetts. Trials ($n = 24$) are listed as individual trapping web site, year (last two digits), and session ("s"), if applicable.

Trial	Ring 1		Ring 2		Ring 3		Ring 4		Ring 5		Ring 6		Ring 7		Total
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
Web0696	0	0	0	0	2	0	1	0	0	2	0	0	2	1	8
Web3eb97	0	0	2	0	1	1	1	1	2	1	0	0	1	1	11
Web1296	0	0	0	0	0	0	0	0	4	0	0	1	2	5	12
Web2eb97	1	0	0	1	1	1	0	1	2	0	2	1	3	0	13
Web0296	1	0	0	1	1	0	0	0	3	0	1	0	5	4	16
Web1eb97	0	1	3	2	2	3	2	3	7	5	0	1	2	2	33
Web1297s2	1	0	1	0	2	1	2	2	5	2	6	0	8	6	36
Web2se97	3	1	0	1	2	2	7	3	2	4	5	3	3	4	40
Web0297s2	1	0	0	3	4	0	1	3	7	2	4	1	11	5	42
Web1se97	1	0	4	1	3	4	7	3	5	2	8	4	4	1	47
Web0497s2	0	1	1	1	2	2	1	1	4	5	8	6	14	9	55
Web2bf98	0	0	3	1	3	1	5	5	1	5	5	12	9	7	57
Web3se97	1	0	1	1	3	5	4	2	9	6	9	11	14	12	78
Web1bf98	1	1	1	5	7	6	6	5	9	7	4	10	19	12	93
Web1298s2	0	0	3	5	2	4	11	7	8	8	10	8	13	24	103
Web2eb98	2	1	5	2	2	6	6	4	10	9	13	9	20	14	103
Web3se98	3	4	4	2	6	6	3	5	5	12	14	11	11	17	103
Web0698s2	1	0	2	2	7	1	9	12	10	4	9	10	26	18	111
Web1eb98	3	3	5	5	5	4	7	10	8	12	9	10	15	21	117

Web3eb98	3	6	6	5	2	7	8	8	14	20	8	11	22	16	136
Web0298s2	2	2	4	6	7	12	10	11	12	12	15	9	23	17	142
Web0498s2	3	0	5	7	7	3	10	14	16	13	15	14	27	27	161
Web1se98	5	2	9	14	14	9	13	7	9	19	23	14	24	30	192
Web2se98	6	12	10	16	22	9	26	26	26	23	19	24	32	33	284
Total	38	34	69	81	107	87	140	133	178	173	187	170	310	286	1,993

TRAPPING WEB FREQUENCIES OF INDIVIDUAL RED-BACKED VOLES

Trapping web capture frequencies of individual red-backed voles per sex per trapping web ring, sorted by total captured; all ages included. Voles were live-trapped at 12 individual trapping webs at seven sites from 1996-98, in central Massachusetts. Trials ($n = 23$) are listed as individual trapping web site, year (last two digits), and session ("s"), if applicable.

Trial	Ring 1		Ring 2		Ring 3		Ring 4		Ring 5		Ring 6		Ring 7		Total
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
Web2eb97	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Web0296	0	0	0	0	0	0	0	1	1	2	2	0	0	1	7
Web0696	0	0	1	0	0	1	1	0	1	1	0	1	2	1	9
Web1eb97	2	2	0	1	1	1	3	1	0	0	0	0	0	0	11
Web2se97	0	0	0	1	1	1	2	1	1	1	2	2	1	0	13
Web0298s2	0	0	2	1	2	1	0	1	1	2	2	0	1	2	15
Web3eb97	1	0	2	5	0	2	0	0	1	1	3	0	0	0	15
Web0498s2	1	2	1	1	1	2	1	3	1	1	1	0	3	1	16
Web1297s2	0	0	1	0	1	1	0	0	2	1	2	4	0	0	16
Web0497s2	1	0	3	1	1	2	3	1	2	3	0	1	0	3	18
Web1298s2	1	0	1	0	2	2	1	2	1	1	2	5	0	3	21
Web1296	0	0	3	0	1	2	1	0	2	5	1	3	7	3	28
Web2eb98	0	0	1	3	3	4	0	1	7	3	3	2	4	4	35
Web1eb98	3	1	3	2	1	4	1	5	4	1	3	3	4	3	38
Web1se97	1	0	1	1	2	2	3	2	9	5	5	4	2	1	38
Web3se98	3	1	3	4	4	3	2	7	4	2	6	1	5	0	45
Web0698s2	1	0	4	2	4	0	3	7	4	4	7	5	3	3	47
Web2bf98	0	3	3	2	1	6	1	5	5	7	6	0	3	7	49
Web3eb98	1	1	4	5	3	2	2	7	1	1	8	8	5	5	53

Web2se98	3	0	5	3	11	7	3	7	2	5	3	6	6	6	67
Web3se97	3	6	10	6	6	8	7	8	6	3	3	3	1	1	71
Web1se98	1	2	2	3	6	10	9	10	8	12	14	13	7	16	113
Total	24	25	53	47	53	62	50	71	66	66	77	68	57	66	785

TRAPPING WEB FREQUENCIES OF INDIVIDUAL WHITE-FOOTED MICE BY AGE

Trapping web capture frequencies of individual white-footed mice per age per trapping web ring, sorted by total captured; both sexes included. Mice were live-trapped at 12 individual trapping webs at seven sites from 1996-98, in central Massachusetts. Trials ($n = 24$) are listed as individual trapping web site, year (last two digits), and session ("s"), if applicable.

Trial	Ring 1		Ring 2		Ring 3		Ring 4		Ring 5		Ring 6		Ring 7		Total
	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	
Web0696	0	0	0	0	0	2	0	1	0	2	0	0	1	2	8
Web3eb97	0	0	2	0	2	0	2	0	2	1	0	0	1	1	11
Web1296	0	0	0	0	0	0	0	0	3	1	0	1	6	1	12
Web2eb97	1	0	1	0	1	1	1	0	0	2	3	0	0	3	13
Web0296	1	0	0	1	0	1	0	0	2	1	1	0	3	6	16
Web1eb97	0	1	4	1	3	2	4	1	5	7	1	0	3	1	33
Web1297s2	1	0	0	1	0	3	2	2	5	2	5	1	11	3	36
Web2se97	1	3	0	1	1	3	4	6	4	3	3	5	5	2	41
Web0297s2	1	0	0	3	0	4	2	2	4	5	3	2	10	6	42
Web1se97	0	1	0	5	2	5	7	3	2	5	6	6	3	2	47
Web0497s2	1	0	1	1	3	1	1	1	3	6	11	3	19	4	55
Web2bf98	0	0	1	3	1	3	5	5	2	4	10	7	10	6	57
Web3se97	0	1	0	2	5	3	2	5	9	7	8	12	12	14	80
Web1bf98	0	2	2	4	4	9	6	5	4	12	8	6	21	11	94
Web3se98	3	4	3	3	8	4	8	0	16	1	17	8	20	8	103
Web1298s2	0	0	8	0	5	1	17	1	14	2	14	4	33	5	104
Web2eb98	3	0	3	4	6	2	6	4	13	7	14	8	25	9	104
Web0698s2	1	0	3	1	6	2	18	3	13	1	17	2	37	7	111
Web1eb98	6	0	10	2	7	4	14	3	16	5	17	2	33	6	125
Web3eb98	4	5	7	4	7	2	10	6	21	13	17	2	34	4	136

Web0298s2	4	0	6	4	12	7	11	10	18	6	21	3	32	8	142
Web0498s2	3	0	10	2	8	2	21	3	23	8	20	9	47	9	165
Web1se98	2	5	10	13	9	14	11	9	17	11	23	14	40	14	192
Web2se98	9	10	9	18	14	17	25	28	24	27	27	16	39	26	289
Total	41	32	80	73	104	92	177	98	220	139	246	111	445	158	2,016

TRAPPING WEB FREQUENCIES OF INDIVIDUAL RED-BACKED VOLES BY AGE

Trapping web capture frequencies of individual red-backed voles per age per trapping web ring, sorted by total captured; both sexes included. Voles were live-trapped at 12 individual trapping webs at seven sites from 1996-98, in central Massachusetts. Trials ($n = 23$) are listed as individual trapping web site, year (last two digits), and session ("s"), if applicable.

Trial	Ring 1		Ring 2		Ring 3		Ring 4		Ring 5		Ring 6		Ring 7		Total
	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	Adult	Non-adult	
Web2eb97	1	1	0	0	0	0	0	0	0	0	0	0	0	1	3
Web0296	0	0	0	0	0	0	1	0	3	0	2	0	1	0	7
Web0696	0	0	1	0	1	0	1	0	2	0	1	0	0	3	9
Web1eb97	4	0	1	0	2	0	3	0	0	0	0	0	0	0	10
Web2se97	0	0	1	0	2	0	3	0	1	1	5	0	1	0	14
Web3eb97	1	0	3	4	0	2	0	0	0	2	3	0	0	0	15
Web1297s2	0	0	1	0	1	1	0	0	1	1	6	0	3	1	15
Web0498s2	3	0	2	0	3	0	4	0	2	0	1	0	1	0	16
Web0298s2	0	0	2	1	3	0	2	0	2	1	2	0	4	0	17
Web0497s2	0	1	4	0	0	3	2	2	2	3	1	0	0	0	18
Web1298s2	1	0	1	0	3	1	3	0	2	0	7	0	3	0	21
Web1296	0	0	2	1	3	0	0	0	6	1	4	0	10	0	27
Web1eb98	4	0	5	0	5	0	3	3	4	1	6	0	7	0	38
Web1se97	1	0	2	0	4	0	4	1	13	2	7	2	3	0	39
Web2eb98	1	0	6	1	6	1	1	0	7	3	4	1	7	1	39
Web0698s2	1	0	4	3	2	2	7	3	7	1	11	1	6	0	48
Web3se98	4	0	6	1	7	1	8	2	6	0	8	1	5	0	49
Web3eb98	2	1	6	3	4	1	8	1	2	0	14	2	11	0	55
Web2bf98	2	1	5	0	5	3	4	3	11	3	5	2	10	2	56
Web1bf98	2	4	6	4	3	0	8	2	6	3	12	1	10	3	64

Web3se97	7	5	12	6	10	8	11	7	6	3	6	1	2	0	84
Web1se98	2	1	5	1	16	1	17	3	19	4	25	4	23	4	125
Total	39	15	83	26	95	27	98	32	107	31	140	15	118	16	842

APPENDIX H

EFFORT AND NUMBERS OF INDIVIDUAL WHITE-FOOTED MICE FROM PAIRED TRIALS

Effort/numbers of individual white-footed mice (*Peromyscus leucopus*) live-trapped during paired trials, 1997-98, on eight, individual 3-ha trapping webs superimposed on eight, square 0.81-ha mark-recapture grids at three forested sites in central Massachusetts. Paired trials ($n = 14$) are listed as site and year, by grid then web. Numbers of radii comprising each web follow the number of live-traps used.

Paired trials (site name/yr)	Numbers of live-traps/radii	Trial duration (days)	Numbers of w-f mice	Trial start date (Julian)
Grid1eb97	49	4	29	338
Web1eb97	168/12	4	34	346
Grid2eb97	49	4	11	346
Web2eb97	84/6	3	13	339
Grid3eb97	49	4	24	338
Web3eb97	168/12	4	11	346
Grid1se97	49	4	37	309
Web1se97	224/16	4	53	316
Grid2se97	49	4	32	309
Web2se97	224/16	4	46	316
Grid3se97	49	4	25	316
Web3se97	224/16	4	80	309
Grid1bf98	49	5	43	307
Web1bf98	196/14	5	94	292
Grid2bf98	49	5	37	292
Web2bf98	196/14	5	65	306
Grid1eb98	49	5	71	275
Web1eb98	168/12	5	127	265
Grid2eb98	49	5	49	265
Web2eb98	168/12	5	112	275
Grid3eb98	49	5	65	275
Web3eb98	168/12	5	137	265
Grid1se98	49	5	64	286
Web1se98	224/16	5	212	300
Grid2se98	49	5	84	299
Web2se98	224/16	5	293	286
Grid3se98	49	5	43	299
Web3se98	112/8	5	111	314

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